Corticocortical Connections of Anatomically and Physiologically Defined Subdivisions Within the Inferior Parietal Lobule

R.A. ANDERSEN, C. ASANUMA, G. ESSICK, AND R.M. SIEGEL

Department of Brain and Cognitive Sciences, M.I.T., Cambridge, Massachusetts 02139 (R.A.A.); N.I.H. Animal Center, Poolsville, Maryland 20837 (C.A.); Dental Research Center, University of North Carolina, Chapel Hill, North Carolina 27514 (G.E.); Department of Neurobiology, Rockefeller University, New York, New York 10021 (R.M.S.)

ABSTRACT

The anatomical and functional organization of the inferior parietal lobule was investigated in macaque monkeys by using anterograde and retrograde anatomical tracing techniques and single cell recording techniques in awake, behaving monkeys. The connections of areas 7a and 7b, and of two previously unexplored areas, the lateral intraparietal area (LIP) and the dorsal prelunate area (DP), were examined in detail. Functional mapping experiments were performed in all four areas.

Prior to this study the pathways for visual input to area 7a were unclear. In these experiments we found several direct projections from extrastriate visual areas, including the lateral intraparietal (LIP), dorsal prelunate (DP), parieto-occipital (PO), and medial superior temporal (MST) areas into area 7a. Using the observed laminar patterns of connections between areas 7a, LIP, and DP and other extrastriate cortical areas, we were able to construct a hypothetical flow of visual information processing from striate cortex to area 7a. A broader hierarchy was also produced, which relates the positions of areas 7a, 7b, LIP, and DP to various cortical fields in the parietal, temporal, and frontal lobes.

By combining single cell recording techniques in trained monkeys with anatomical tracing techniques, we have parcelled the inferior parietal lobule into several subdivisions on the basis of both anatomical and physiological grounds. A clear segregation of visual and somatosensory responses was found in the inferior parietal lobule with areas 7a, LIP, and DP being visual and visual-motor and area 7b being primarily somatosensory. A similar segregation was found anatomically with areas 7a, LIP, and DP being interconnected primarily with other visual cortical areas and area 7b being connected with several somatosensory areas. Area 7b was also found to connect to a few visual cortical areas, and these connections likely account for the small but consistent number of visually responsive cells that are found in this region. Areas LIP, DP, and 7a differed in receptive field and saccade-related properties. Area 7a visual receptive fields were very large and usually bilateral with a small but significant number of them having receptive field centers in the ipsilateral visual field. Area DP and LIP receptive fields were smaller and the receptive field peaks were almost always confined to the contralateral visual field. Areas 7a, DP, and LIP all contained cells with saccade-related responses; however, in area 7a there were fewer saccade cells than area LIP, and presaccadic responses were only observed in area LIP. Consistent with its functional specialization for saccades, area LIP was found to be strongly interconnected with areas involved in saccadic eye movements, including the frontal eye fields and intermediate layers of the superior colliculus, whereas area 7a had only weak connections to the frontal eye fields and had no detectable projection to the superior colliculus. Areas LIP, 7a, and DP neurons were found to have eye-position-related activity. Extensive quantitative experiments showed the distributions of the slopes and directions of the gaze fields were similar in areas 7a and LIP, but the intercepts were larger for area LIP.

Area 7a was found to be connected to at least 22 cortical areas, including MST, superior temporal polysensory (STP), fundus superior temporal (FST), inferotemporal (IT), lateral and

medial TF (TFl, TFm) areas, and TEO in the temporal lobe; LIP, DP, PO, medial intraparietal (MIP), posterior intraparietal (PIP), medial dorsal parietal (MDP), medial PG (PGm), and 7b areas in the parieto-occipital cortex; areas 8a, 46, 45, 11, and supplementary eye fields (SEF) in the frontal lobe; and areas LC and LA in the cingulate gyrus. Area 7b was found to be connected to area 5; the granular insula (IG), PGm, LC, LA, MDP, MST, PO, STP, and IT areas, and areas 45, 6, and 12. Area LIP had corticocortical connections with the PO, DP, 7a, MST, middle temporal (MT), V4, dorsal and ventral V3 (V3d, V3v), V3A, TEO, TF, 8a, and 46 areas. Area DP was connected to V3A, LIP, 7a, V4, MST, PO, 46, and 8a. All corticocortical connections were reciprocal.

The view that emerges from this study is of a densely interconnected network of connections between large numbers of brain regions with each cortical area, including areas 7a, 7b, LIP, and DP, being a single node in this highly distributed and interactive network. An important goal is to determine what different computations are being performed at each node in this network.

Key words: area 7a, area 7b, dorsal prelunate area, lateral intraparietal area, posterior parietal cortex, macaque monkey, extrastriate cortex, visual system

Early associationalist views held that the cortex of the inferior parietal lobule (IPL) was a single area integrating visual and somatosensory information. However, even at the beginning of the twentieth century there was evidence for subdivision of this cortical area into two regions based on cytoarchitecture. Whereas Brodmann ('05) had recognized this region as one area, Vogt and Vogt ('19) further subdivided Brodmann's area 7 into two regions, a medial area 7a and a more lateral area 7b. Von Bonin and Bailey ('47) confirmed this subdivision and labelled the medial area PG and the lateral area PF, using von Economo's ('29) nomenclature for the inferior parietal lobule in man.

Recording experiments in IPL have suggested that there is also a functional distinction between area 7a (PG) and 7b (PF). Hyvarinen and colleagues made systematic maps of the functional organization of IPL and reported that cells in the medial aspect of the gyrus (7a) responded predominantly to visual and visual-motor activities, whereas the more lateral aspect of the gyrus (7b) contained cells predominantly responsive to somatosensory and somatomotor activities (Hyvarinen and Shelepin, '79; Hyvarinen, '81). Unfortunately, these experiments did not employ stimuli and behavioral measures that were rigorously controlled, making it difficult to determine the source of the cells' activity. Robinson and Burton ('80a,b) made extensive maps of area 7b in behaving monkeys and found that a majority of the cells responded to somatosensory stimuli. They reported that, although the receptive fields were large and sometimes could include most of the body, there was a crude somatotopy in area 7b. Thus the experiments of Hyvarinen and colleagues and Robinson and Burton suggest that area 7a is concerned with visual and visual-motor functions whereas area 7b is concerned with somatosensory and somatomotor functions.

Initial anatomical tracing experiments showed IPL to be connected to widespread areas in the frontal, parietal, and temporal lobes (see Lynch, '80; Pandya and Seltzer, '82; Andersen, '87; Goldman-Rakic, '88, for reviews). In recent years, more detailed studies have revealed that there are different sets of connections for different subregions of the IPL and these observations have led to the suggestion that there are several cortical areas within the lobule (Pandya and Seltzer, '82; Andersen, '87; Goldman-Rakic, '88).

The present study has been undertaken in order to advance our knowledge of the inferior parietal lobule by establishing the source of visual inputs, determining the hierarchy of visual information flow from striate cortex to the posterior parietal cortex, and delineating the subdivisions of the inferior parietal lobule based on the systematic study of its functional and anatomical properties. We have

Abbreviations

APN	anterior pretectal nucleus	PIP	posterior intraparietal area
DMZ	densely myelinated zone	PO	parieto-occipital area
DP	dorsal prelunate area	SC	superior colliculus
DPN	dorsal pretectal nucleus	SEF	supplementary eye fields
FB	fast blue	ST	superior temporal sulcus
FEF	frontal eye fields	STP	superior temporal polysensory area
FST	fundus superior temporal area	STS	superior temporal sulcus
Ig	insula, granular area	TAA	tritiated amino acid
IP	intraparietal sulcus	TB	true blue
IPL	inferior parietal lobule	TFl	lateral area TF
IT	inferotemporal area	TFm	medial area TF
HRP	horseradish peroxidase	V1	visual area 1
L	lunate sulcus	V2	visual area 2
LF	lateral fissure	V3	visual area 3
LIP	lateral intraparietal area	V3d	visual area 3, dorsal portion
MDP	medial dorsal parietal area	V3v	visual area 3, ventral portion
MIP	medial intraparietal area	V4	visual area 4
MST	medial superior temporal area	V4t	V4 transitional zone
MT	middle temporal area	V5	visual area 5
NY	nuclear yellow	VIP	ventral intraparietal area
PGm	medial area PG	VP	ventral posterior area

examined in detail the corticocortical connections of the three areas in the inferior parietal lobule—areas 7a and 7b, and the lateral intraparietal area (LIP)—and one region in the adjoining dorsal aspect of the prelunate gyrus—the dorsal prelunate area, DP. These studies were performed using anterograde (tritiated amino acids) transport and retrograde (horseradish peroxidase and fluorescent dye) transport techniques for tracing projection pathways. In order to study the functional organization of these high level cortical areas we have trained and recorded from two awake, behaving monkeys performing various visual and oculomotor tasks and correlated the site of activity with the anatomical data.

The first goal of our study is to determine how area 7a receives visual input. Initially we considered two possible sources, subcortical and corticocortical pathways. We found that area 7a's major thalamic projection is from the medial pulvinar (Asanuma et al., '85); however, this structure receives inputs only from the deep layers of the superior colliculus, which are much more oculomotor in nature than the superficial, visual layers of the colliculus, which do not project to areas of the thalamus which project to area 7a (Benevento and Standage, '83). The only other source of subcortical visual inputs to 7a is from the pretectum via the thalamus, but this projection to area 7a is relatively minor. Thus it seems unlikely that the tremendously visual nature of area 7a can result from these subcortical inputs. It is reasonable to assume then that corticocortical inputs are primarily responsible for carrying visual information to area 7a and that they are derived from primary visual cortex via extrastriate visual cortex; however, the location and nature of this pathway need to be determined. Our study includes an examination of the connections of the relatively uncharted dorsal prelunate area (DP), which lies dorsal to V4 on the prelunate gyrus (Maguire and Baizer, '84; Asanuma et al., '85; Van Essen, '85; May and Andersen, '86), and the recently described area LIP, which lies on the lateral bank of the intraparietal sulcus (Andersen et al., '85a), because observations from our earlier tracing experiments in area 7a (Andersen et al., '85a) have indicated that these unexplored areas of cortex represent a probable major pathway for visual input to area 7a.

The second goal of our study is to determine anatomically the presumed hierarchical flow of visual information processing in the posterior parietal cortex by elucidating the laminar distributions of the sources and terminations of its corticocortical projections. This approach has been successful in earlier parts of the visual pathway, where it has been proposed that feedforward projections originate from cell bodies located in supragranular layers and end in terminals in layer IV and lower layer III, and feedback projections originate in the supragranular and infragranular layers and end most densely in layers I and VI (Rockland and Pandya, '79; Maunsell and Van Essen, '83). As will be shown in the results, we are able to trace a hierarchy of visual processing from area VI on the bottom of the hierarchy, to area 7a on the top by making one modification to this scheme for the projections into the posterior parietal cortex: feed-forward projections originate in both superficial and *deep* cortical layers but still end predominantly in layers IV and lower layer III.

The third major objective of this study is to provide evidence for the subdivision of IPL into several cortical areas and to define the connections of these areas. To these ends, the entire constellation of corticocortical connections of area 7a, 7b, DP, and LIP has been examined with emphasis placed on differences in corticocortical connectivity. Previous experiments from our laboratory have shown these regions to have very different patterns of thalamocortical-corticothalamic (Asanuma et al., '85) and corticopontine (May and Andersen, '86) connectivity. Finally, in three hemispheres we did detailed mapping of the functional organization of IPL prior to injection of tracers to correlate the functional organization of the areas with the subdivisions made on anatomical grounds. The mapping experiments involved recording single cell activity in awake, behaving monkeys who were performing behavioral tasks under highly controlled conditions. These experiments revealed different functional properties for the various areas consistent with their differences in anatomical connectivity.

MATERIALS AND METHODS
Data base

Twenty-five separate anatomical tracing experiments were performed in 19 hemispheres of ten cynomolgus monkeys (*Macaca fascicularis*) and two rhesus monkeys (*Macaca mulatta*). Anterograde tracing experiments used a mixture of tritiated amino acids (leucine and proline); the retrograde tracing experiments used the fluorescent dyes fast blue (FB), true blue, and nuclear yellow (NY), and the enzyme horseradish peroxidase. Experiments were performed in areas 7a (twelve cases), 7b (three), DP (three), LIP (three), and 8 and 46 of Walker in the prefrontal cortex (four). Some of these cases were also used in studies of thalamocortical (Asanuma et al., '85), corticopontine (May and Andersen, '86), and callosal connections (Andersen et al., '85a). Table 1 summarizes where the various tracers were injected.

For area 7a two cases involved NY and four FB, allowing for a direct comparison of their relative selectivity and sensitivity for transport (Table 1). No obvious differences were found for labelling with the two tracers. This result contrasts with the results of single injection cases of HRP and FB made into area LIP. It was found that FB was much more sensitive as judged by more labelled neurons, and weak labelling in areas that did not appear labelled with HRP injections. It is unlikely that this latter result is due to greater tracer diffusion, since the labelling at the FB injection sites appeared to be smaller in volume than at the HRP injection site.

Anterograde tracing techniques

Craniotomies were made over the posterior parietal cortex and, in the four dye injections in the frontal lobe, over the prefrontal cortex. All surgical procedures were performed with full aseptic precautions with the animals anesthetized with sodium pentobarbital (35 mg/kg). A mixture of equal parts ^{3}H-proline (L 2-, 3-, or 5-^{3}H-proline, specific activity 13 or 17 Ci per mmol) and ^{3}H-leucine (L 4- or 5-^{3}H-leucine, specific activity 47 Ci per mmol) was evaporated to dryness

TABLE 1. Summary of Where Tracers Were Injected[1]

	Tracer					
	TAA	NY	FB	TB	HRP	Total
7a	5	2	4	1		12
7b	2		1			3
DP	2	1				3
LIP	1		1		1	3
Frontal lobe		4				4
Total	10	7	6	1	1	25

[1]12 monkeys, 19 hemispheres.

and then reconstituted in sterile saline to yield a final activity of 100 μCi/μl. Single or multiple injections of .05 to .5 μl of this mixture were made into the cortex over periods of 15–30 minutes through a 1.0 μl Hamilton syringe. After survival periods of 2–7 days, all of the animals were anesthetized with ketamine followed by a lethal dose of nembutal, then perfused transcardially with cold, heparinized saline followed by 10% formalin in 0.1 M phosphate buffer (pH 7.5). After a period of fixation in this solution, three of the brains were photographed, blocked, dehydrated, embedded in Paraplast, and serial sectioned at 25 μm thickness. For the perfusion of the remaining brains the saline and formalin solutions were followed by an 8% sucrose, 10% buffered formalin solution. The brains were then photographed, cut into four blocks, and placed in a 15% sucrose, phosphate buffered, saline solution for 36 hours prior to sectioning on a freezing microtome at 30 μm thickness.

Every ninth section was mounted on gelatinized slides, defatted, hydrated, and coated with Kodak NTB-2 emulsion as described by Cowan et al. ('72). After exposure for 4–12 weeks at 4°C, the autoradiographs were developed in Kodak D19, fixed, and stained through the emulsion with 0.5% thionin at low pH.

Projection drawings of the sections were made with a Beseler projection apparatus equipped with an ultraviolet filter at magnifications of ×7.5 or ×10. The analysis of cytoarchitecture was made through a Wild dissecting microscope equipped with a camera lucida, and the terminal labeling was plotted under a compound microscope. The injection site was considered to include the entire zone in which the silver grains were evenly and densely accumulated over both cell bodies and neuropil. Terminal labelling was assumed at regions where there was dense labelling in the neuropil distant from the injection site.

Retrograde tracing techniques

The fluorescent markers used in these experiments were nuclear yellow (NY), fast blue (FB), and, in one case, true blue (TB) (Fig. 1). Single or multiple injections of .05 to .5 μl of 2% aqueous solutions of NY or 5% FB or TB were made under visual control using a Zeiss stereo surgical microscope. For the larger injections, a 1 μl Hamilton syringe was used. Smaller injections were made with a pulsed air pressure system through a calibrated glass micropipette. Injections were administered over a period of 10–30 minutes. Often two dyes were injected in different cortical locations in the same animal to enable a direct comparison of the different labelling patterns. Survival times were 2 weeks for the FB and TB and 2–5 days for the NY. The animals were reanesthetized and perfused and their brains were prepared for frozen sectioning in the manner described above for the autoradiographic experiments.

The brains were sectioned on a freezing microtome at 30 μm. Two series of every ninth section (intervals of 270 μm) were mounted with one series being used for fluorescence photomicrography and the other used for plotting labelled cells. These two series were taken from adjacent sections and one of these series was also adjacent to the autoradiographic series. The six intervening sections were stored at 4°C in buffered formalin solution. In one case, brain 8, every sixth section was used (180 μm intervals). The sections were immediately mounted from water after sectioning and were dried with circulating air to prevent tracer diffusion. After drying they were stored at 4°C in light-sealed boxes that contained cannisters of desicant to prevent the background fluorescence that occurs when the sections absorb water.

The sections were viewed with a Leitz Orthoplan fluorescence microscope. Color photomicrographs were made of many of the sections and labelled cells in each section, or every other section, of one series were plotted either under direct observation or with the use of a computerized plotting system. The latter system consisted of high precision potentiometers connected to the head stage of the microscope that gave the two-dimensional location of labelled cells. These coordinates, and the outline of the section, were stored on computer disk and outputted to a printer to create hardcopies.

After plotting was complete the sections were defatted, rehydrated, and stained with thionin. In several experiments a separate series was mounted and stained for myelin according to the method of Gallyas (Gallyas, '79).

In one case a 0.5 μl injection of horseradish peroxidase (HRP) was made into area LIP and the brain was processed according to the TMB method of Mesulam et al. ('77).

Two-dimensional reconstructions

Flattened reconstructions were made of the posterior parietal cortex (Figs. 2, 8, 13), prefrontal cortex (Fig. 19), superior temporal sulcus (Fig. 10), and cingulate cortex (Fig. 11). The degree of areal distortion was kept to a minimum by flattening only the relevant areas of the brain as opposed to flattening the entire brain. Initial flattenings were made using three-dimensional models of the cortical areas. Bare wires were molded to the outlines of layer IV that were drawn from the magnified projections of the Nissl stained sections that were used to plot label. The wires were then soldered to cross wires in sequence forming a skeleton of the three-dimensional shape of the cortex. This skeleton was covered with plastic tape, painted with latex, and cured in an oven. The contours of the wire sections, as well as the lips and fundi of the sulci, were drawn onto the cured sheet of latex before it was removed from the wire and tape mold. Small cuts were made in the latex to facilitate its flattening. The section outlines and sulci were transferred from the flattened latex to tracing paper, as well as the label drawn on the original plots of the sections.

By using this latex model method of reconstruction, we were able to get a good estimate of the amount of areal distortion in our reconstructions. These areal distortions were small, being under 5% in most cases. The absence of appreciable areal distortion is due to rather small sections of cortex being flattened, and angular distortions not being minimized. Once we had obtained the flattened shape of the cortex by using this direct molding method, we compared it to the paper and pencil method of Van Essen and Maunsell ('80) and found that both techniques gave similar results. In subsequent reconstructions we then used the simpler paper and pencil technique.

Figure 2 shows a flattened reconstruction of the posterior parietal cortex that used the direct, latex model method. Figure 2A shows the block of the cortex that is to be flattened, which includes the prelunate gyrus and inferior parietal lobule. Figure 2B shows the general relative movement of the gyral and sulcal landmarks that result from flattening. The shaded area in Figure 2C shows that much of the area of interest lies buried in sulci, and Figure 2D shows the major subdivisions recognizable in our material.

Methods—electrophysiology

In monkey number 15 we made extensive single cell recordings from both hemispheres prior to making small (.05 μl) injections of retrograde tracer in both area 7a's.
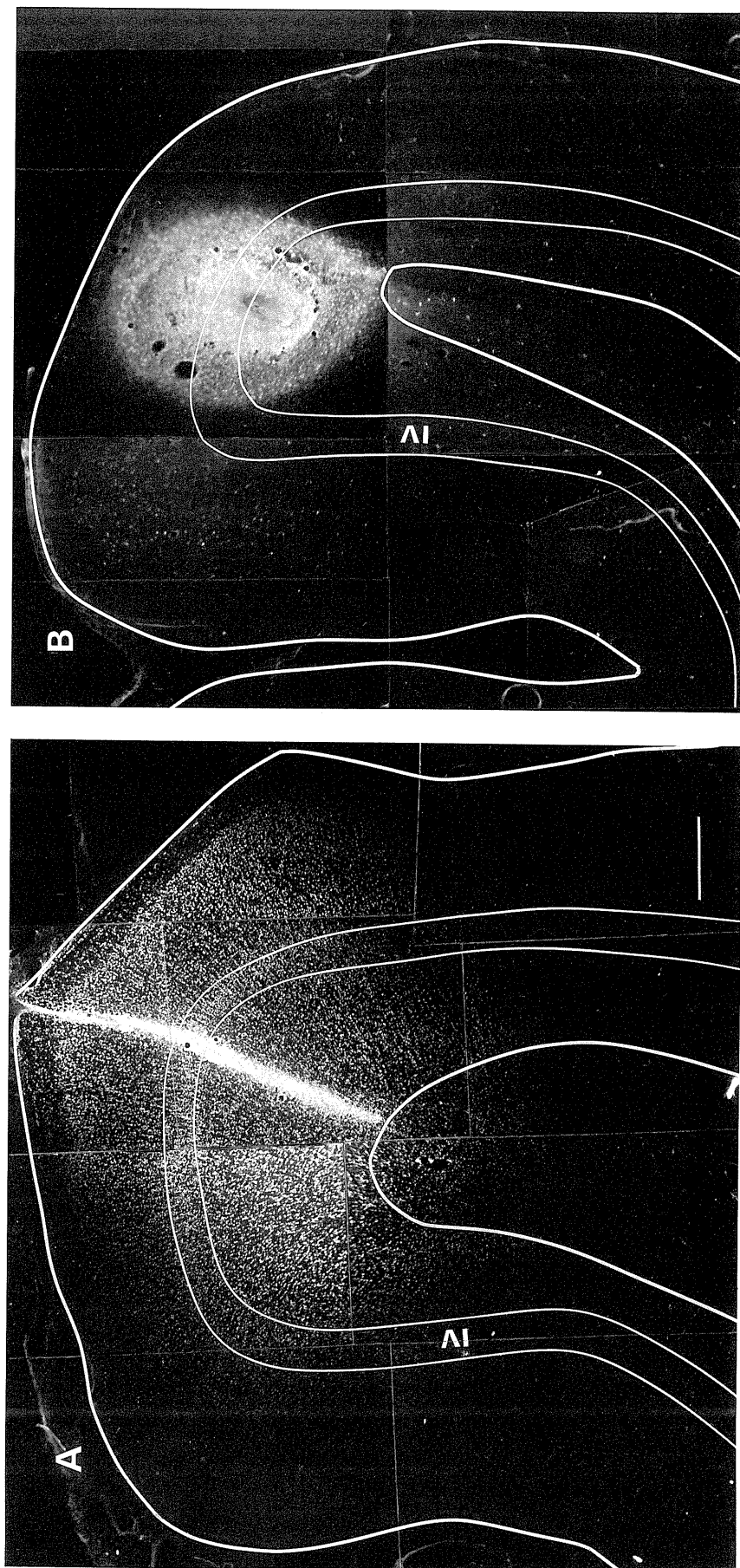
Fig. 1. Fluorescence photomicrographs of two retrograde tracer injection sites. A: Site of a .05 μl injection of nuclear yellow into area 7a of the right hemisphere of case 15. B: Site of a .05 μl injection of fast blue into area 7a of the left hemisphere of case 15. In both cases the white lines outline the thickness of the cortex in coronal section and the location of layer IV. Note that both injection sites are small and completely contained within the cortex. The inferior parietal lobules of both hemispheres were extensively mapped using single cell recording techniques in trained monkeys prior to the injections. The bar indicates 500 μm.
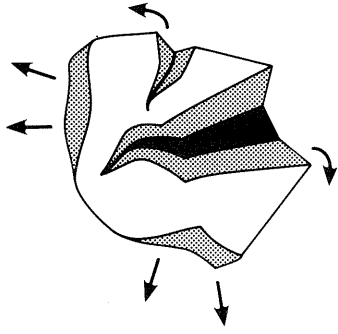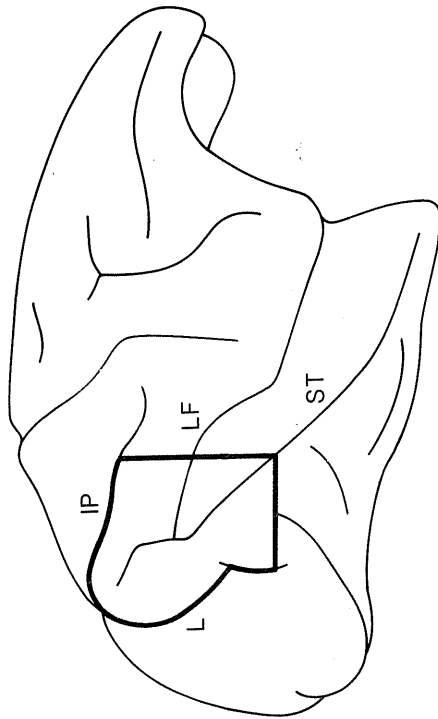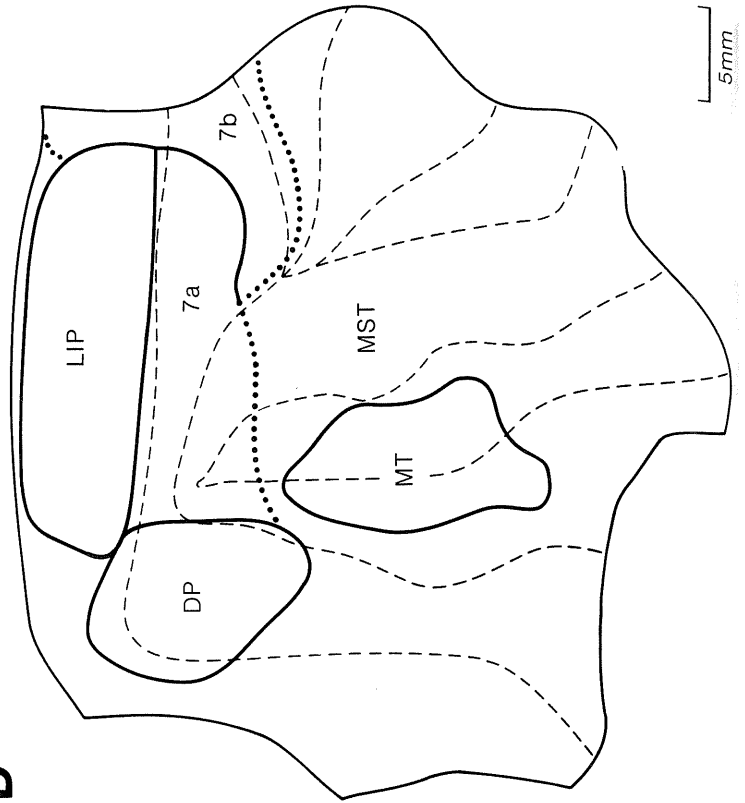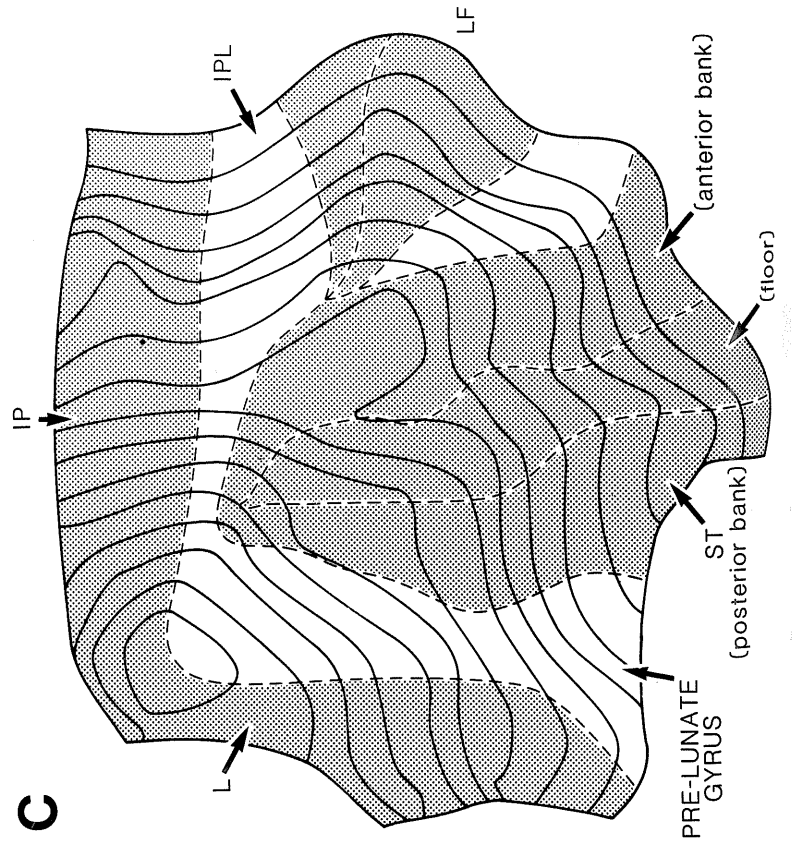
Nuclear yellow was injected in the right hemisphere and fast blue was injected in the left hemisphere; the injection sites are shown in Figure 1. Recording experiments were also performed in one hemisphere from a second monkey (83-1) in which no anatomical tracers were injected. The two monkeys were trained to do various oculomotor tasks, and the single cell recordings were made while they were performing these tasks; the details of the behaving monkey recording techniques are outlined below. Eighty-three penetrations were made over a period of 4 months from the right hemisphere of monkey 15, sixty-seven penetrations made from the left hemisphere of monkey 15 over a period of 3.5 months, and twenty-four penetrations were made in the left hemisphere of monkey 83-1 over a 30 day period. Four hundred eight cells were studied quantitatively in computer controlled experiments from these three hemispheres. Histological reconstruction of the electrode tracks indicated that recordings were made from areas 7a, 7b, LIP, DP, area 5, and MST (Fig. 20).

Behavioral and training tasks

The animals were trained to perform a fixation-dimming detection task. The appearance of a fixation target initiates a trial; the trial proceeds if the animal pulls back on a response key and the trial ends when the animal releases the key indicating that he has detected the dimming of the fixation stimulus. If the animal's response is within a reaction-time window after the fixation point dims he receives a drop of juice as a reward, but if he misses the response window he receives no reward and no punishment. During training the animals were water deprived in their cages and received all their fluid in the training sessions. Fluid intake is maintained through either rewards or supplement after training. To ensure that the animals do not employ timing cues, the intertrial intervals and foreperiods are varied.

Training took place in the recording chamber. The animals sat in a primate chair and viewed stimuli presented under computer control. The animals' behavior was shaped in daily training sessions of 2–3 hours each that were almost entirely automated. The animals first learned to pull the lever in response to the fixation light and then only to release the lever when the light dims. The animals then learned to detect smaller and smaller dimmings of the fixation light until they could detect changes that were difficult to notice for untrained human observers. Simultaneously they learned to work at longer and longer foreperiods until they could operate at 90% accuracy over a randomized set of foreperiods ranging from 500–5,000 msec.

Next a surgical procedure was performed in which a restraining bar was mounted on the skull and a search coil for monitoring eye position was implanted on the globe of one eye by the method of Judge et al. ('80). After 1 week to recover from the surgery, the animals were trained to perform the following tasks: 1) to track visually a moving fixation target; (2) to make saccades to new fixation targets if the initial target is extinguished; (3) to maintain fixation of the fixation point and to ignore the appearance of visual test stimuli. Eye movement recordings were made during training. In the case of inappropriate eye movements, such as looking at the visual test stimuli, the trials were cancelled without reward and the animals quickly learned the correct oculomotor behaviors. Monkey 15 was trained in three special tasks:

Maintained fixation without fixation targets. The animal was trained to maintain fixation in total darkness. The eye positions were monitored, and if, during the target-free period of the trial, the animal broke fixation the trial was aborted.

Prism task. The animal fixated the fixation point on the target screen while looking through prisms in the light. By changing the diopter values of the prisms the animal was required to gaze at different angles to fixate the target. Under these conditions, the retinotopic location of the background does not change, since the fixation point is not moved with respect to the visual background, and yet the animal fixates at different eye positions.

Memory-saccade task. In the third special task, the animal was trained to withhold a saccade to a concurrent target until the fixation point was turned off. The animal was required to maintain fixation of the fixation target even though a second peripheral fixation target appeared. At a variable time between 500 and 1,500 msec after the appearance of the second fixation point, the first fixation point disappears, thus commanding a saccade to the second point. Sixty milliseconds after the first target went off, the second target also went off and did not reappear until 300 msec later. Thus the animal made the saccade in complete darkness. The animal learned this task easily and made accurate saccades to the remembered position of the second target. The second target dimmed for detection and reward a variable period after its reappearance. In later experiments the target was flashed only briefly, being extinguished at least 500 msec before the offset of the fixation point commanding the saccade. Under these conditions the animal was required to memorize the spatial location of the saccade. These experiments were performed in the dark and catch trials in which no target was flashed and no saccade was made were used to rule out the possibility that the activity was related to the offset of the fixation point.

The above tasks were used to assess whether cells had visual-, saccade-, or eye-position-related activity. It was generally found that area 7a and LIP neurons were light-sensitive but that many of the cells also had eye-position-and saccade-related activity. The eye-position activity could be assessed without contaminating visual artifacts in the special fixation without fixation point and prism tasks. In the former task, the cell's activity is monitored with the eyes in different positions and the animal is required to fixate the remembered location of the visual target at these different eye positions. The prism task is unique among the other two tasks in being performed in the light; however, since the retinotopic location of the fixation point and visual backgrounds do not change with eye position this task also

Fig. 2. Parcellation of inferior parietal lobule and adjoining dorsal aspect of the prelunate gyrus used in this study. The cortical areas are represented on flattened reconstructions of the cortex. **A:** Lateral view of the monkey hemisphere. The darker line indicates the area to be flattened. **B:** The same cortex isolated from the rest of the brain. The stippled areas are cortex buried in sulci, and the blackened area is the floor of the superior temporal sulcus. The arrows indicate movement of local cortical regions resulting from the mechanical flattening. **C:** The completely flattened representation of the same area. The stippled areas represent cortical regions buried in sulci and the contourlike lines are tracings of layer IV taken from frontal sections through this area. **D:** Locations of several of the cortical areas. The dotted lines indicate borders of cortical fields that are not precisely determinable. From Andersen ('87).

isolates eye-position-related activity. The special saccade task requires the animal to saccade to a remembered location of a target in total darkness and is a good task to evaluate saccade-related activity in the absence of visual stimulus induced activity. With the aid of these tasks, many cells have been found to have saccade-related or eye-position-related activity, and a majority of them also respond to visual stimuli. These results have been reported previously in Andersen et al. ('87). In these experiments we were interested in the spatial distribution of these properties with respect to the different anatomically defined areas of the posterior parietal cortex.

Somatosensory activity was evaluated by gently brushing or palpating the animals' skin and underlying tissue and by flexing and extending the limbs at the joints. Reach-related activity was assessed by having the animal reach for raisins.

Two to three days prior to the beginning of recording, the animals underwent a second operation in which a recording chamber was placed over an opening in the skull centered over the caudal inferior parietal lobule. After the completion of recording in the first hemisphere of monkey 15 a second chamber was placed on the contralateral side in a third surgical procedure.

Recording room

The recording room is sealed and light-tight. The room is 5 ft wide by 11 ft long and is divided in half by a large 8 ft high gray, patternless backprojection screen. Behind the projection screen is an optical bench with three projectors under computer control. The animals face the projection screen at a distance of 53 cm and sit in a plastic primate chair surrounded by the 3 ft by 3 ft plexiglass cube of the quadrature coils. The animals have 90° × 90° unrestricted view of the screen.

The rear and front of the screen are illuminated by four tracks of small floodlights, the outputs of which are adjusted with variable voltage DC power supplies. The room lighting is adjusted for an even screen luminosity measured at the animal's eyes. The animals' behavior is observed from outside the recording room with a closed circuit infrared sensitive video system. There are infrared illuminators in the room so the animals can be monitored with the video system with the room lights off.

Stimulus

The projectors consist of tungsten source light boxes whose outputs are collimated, directed through electronic shutters and slit apertures, reflected off sets of two orthogonal mirror galvanomotors, reflected off a second 1 × 1 meter surface mirror to extend the light path, and focused on the screen. In the collimated part of the light path on two of the projectors are optical mesh screens whose angles with the light path are controlled by galvanometers. These mesh screens are used for dimming the fixation points in the dimming detection task and are also used to adjust the brightness of the stimulus as a function of screen position such that the visual stimuli are always of equal luminosity, regardless of screen position, measured from the animal's eyes with a photometer.

The light sources (250 W tungsten filament incandescent bulbs) are powered by variable DC supplies so that the maximum light outputs can be balanced for the three projectors regardless of the individual characteristics of the bulbs. The filaments are adjustable in all three dimensions, and there is an adjustable spherical mirror behind each bulb

to gather the maximum light. Stimulus intensities ranged from 10 to 40 cd/m^2 and, in those experiments performed in the light, the background was 1–2 cd/m^2. Tests were made in darkness by turning off the track lights.

Recording methods

The recording sessions were limited to 6–7 hours daily with occasional rest periods in which the animals' heads were freed to move in the horizontal plane. During the recording sessions the animals performed 1,000–2,000 trials. Generally, a recording session consisted of a single penetration in which 3–5 units were studied thoroughly.

At the beginning of each recording session, the head was fixed, the plug was removed from the recording chamber, the dura was cleaned (under aseptic conditions) and flushed with a saline-antibiotic mixture, and a mechanical micro-drive was attached to the oil-filled and hydraulically sealed chamber. A polar coordinate system allowed the electrode to be positioned at more than 700 positions in the 18 mm diameter chamber. The minimum advancement of the electrode was a 1 μm increment.

The electrodes were etched, platinum-irridium, and glass coated with an impedance of 2 to 4 MΩ at 1,000 Hz for quantitative single unit studies. The action potentials were amplified and displayed through a head stage, power amplifier, high frequency roll-off filter, differential amplitude discriminator, and audio amplifier. The spikes were stored as interspike time intervals on magnetic disks with a resolution of 0.1 msec. Eye-position data were recorded as both horizontal and vertical eye positions at 100 or 500 Hz.

The laboratory was interfaced with a Digital Equipment Corporation PDP 11/34A digital computer; this computer was wholly dedicated to the laboratory. The presentation of stimuli, the monitoring and recording of behavioral events, and the collection of neural and eye-position data were all under computer control. All these tasks were executed by single collection programs that were operated from a keyboard monitor in the laboratory.

Reconstructing penetrations

At different depths for each penetration at the conclusion of daily recording sessions small electrolytic lesions were made by passing a 4 μA DC current for 4 seconds through the recording electrode with the tip positive. At the end of recordings, guide wires were lowered into the brain at selected chamber coordinates in both hemispheres and the animal was sacrificed. The guide wires were used as landmarks for blocking the inferior parietal lobule and for determining the approximate locations of penetrations that were made early in the recordings whose marking lesions may have disappeared. In our experience the electrolytic lesions are only visible for at most 6 weeks after they are made. Thus, just before the end of the experiment we made several recording penetrations from both sides with electrolytic lesions at the ends of the tracks. A good agreement was found between the predicted location of lesions made from the coordinate system of the microdrive and the actual location of the lesion.

Determination of areas by myeloarchitectural and cytoarchitectural criteria

Areas that were delineated by cytoarchitectural and myeloarchitectural borders in the posterior parietal cortex and adjoining cortex included areas 7a, 7b, MST, MT (V5),

V4t, V4, DP, LIP, and VIP. The locations of many of these regions with respect to the gyral anatomy are shown in Figure 2, and the myeloarchitecture of several of these areas is shown in Figure 3. All cases were Nissl stained, and cytoarchitectural criteria were used for all experiments. Several cases were stained for myelin, and myeloarchitectural criteria were used for determining areas in Figures 1, 2, 4, 5, 17, 20, 21, and 27.

Within the lateral bank of the intraparietal sulcus is area LIP which is myeloarchitecturally heterogeneous (Fig. 3). Area LIP was first described by Andersen et al. ('85a) as the area within the intraparietal cortex that projects most strongly to the frontal lobe. The majority of area LIP makes up a densely myelinated area on the posterior aspect of the lateral bank of the sulcus (Fig. 3). This area is as densely myelinated as area MT with dense myelination through layers III–VI. The separation between the inner and outer bands of Baillarger are less clear in this region of the lateral bank (Seltzer and Pandya, '80). This densely myelinated region is approximately 3–4 mm wide, running from dorsal to ventral in the sulcus and approximately 10 mm long in the rostrocaudal dimension (Ungerleider and Desimone, '86b; Blatt et al., '90). Anteriorily it is bordered by a less densely myelinated area 7b, and posteriorly it becomes less clearly distinguished in the region where the intraparietal and occipitoparietal sulci join. Ventrally it is bordered by the ventral intraparietal area (VIP), a region in the fundus of the intraparietal sulcus first described by Maunsell and Van Essen ('83) on the connectional grounds of receiving area MT projections. (A projection from MT to the posterior parietal cortex was first described by Spatz and Tigges, '72.) The border between VIP and LIP can be distinguished by the relatively lighter myelin staining of area VIP. Dorsally area LIP is bordered by a less densely myelinated area 7a. Recording experiments by Blatt et al. ('87) and Gnadt and Andersen ('88) suggest that area LIP may extend beyond the dorsalmost extent of the densely myelinated area by one or two millimeters. The densely myelinated portion of area LIP appears at least to partially overlap area POai of Seltzer and Pandya (Colby et al., '88), although it does not extend as far anteriorly as POai (Ungerleider and Desimone, '86b). In terms of total area, LIP encompasses about one half of area POa.

Area 7a joins LIP dorsally in the intraparietal sulcus and extends onto the gyral surface of the posterior half of the inferior parietal lobule. It extends across the gyral surface of the inferior parietal lobule and into the caudal aspect of the superior temporal sulcus to join area MST near the dorsal border of its densely myelinated zone (DMZ; Ungerleider and Desimone, '86a). Area 7a borders the dorsal prelunate area (area DP) posteriorly where the prelunate gyrus joins the inferior parietal lobule, and borders area 7b anteriorly. Area 7a can be distinguished by its distinctive bundles of radially oriented, darkly stained fibers (Fig. 3). In Nissl stained sections the cell bodies of area 7a align in radial strings, presumably between the densely staining myelin bundles. Another distinguishing feature in Nissl stained material is layer III of area LIP, which has a sparse upper layer III and dense, large cell lower layer III. This difference gives it a more bilaminar appearance than layer III of area 7a.

The border between area 7a and MST in the superior temporal sulcus is marked by the medial (closer to the upper lip of the sulcus) border of the densely myelinated zone (DMZ) of area MST (Fig. 3). This DMZ area was originally described by Newsome and Wurtz ('82) and was included as part of area MST by Ungerleider and Desimone on the basis of its similar receptive field properties and inputs from MT (Ungerleider and Desimone, '86a; Desimone and Ungerleider, '86). Their peripheral field representation of area MT (area MTp) also included a small portion of this DMZ region (Ungerleider and Desimone, '86a). The anterior border of area 7a with 7b can be distinguished on cytoarchitectural grounds (Vogt and Vogt, '19; Von Bonin and Bailey, '47). In particular, layer V of area 7a is more homogeneous, with area 7b having a sparser lower layer 5 and a dense, large cell upper layer abutting layer IV. There is a distinct functional boundary that corresponds to this cytoarchitectural border, with somatosensory responses recorded on the 7b side and visual responses on the 7a side (see Andersen et al., '87; Fig. 4B). The anterior border of area 7b with SII was determined cytoarchitecturally according to the criteria of Robinson and Burton ('80a). Cortical areas within the insula were identified cytoarchitecturally according to Robinson and Burton ('80a) and Mesulam and Mufson ('82a).

The dorsal prelunate area was first suggested to be a separate area by Maguire and Baizer ('84) on physiological grounds. They found that cells located on the most dorsal aspect of the surface of the prelunate gyrus were distinct from V4 in having large receptive fields and no apparent retinotopic organization. This area was subsequently named the dorsal prelunate area (DP) (Asanuma et al., '85; Van Essen, '85; May and Andersen, '86). Area DP can be distinguished cytoarchitecturally from area 7a by its much denser layer IV and its more poorly differentiated layers V and VI. Myeloarchitecturally, the inner and outer layers of Baillarger of area DP are thinner and darker staining than those in area 7a. The lateral border with V4 is difficult to detect with myelin or Nissl stains and is defined here as the ventral limit of the dorsal prelunate zone projecting to area 7a. This region probably does not include area Opt of Pandya and Seltzer ('82), which instead appears to comprise the dorsal-posterior aspect of area 7a.

Other visual areas delineated by relatively heavier myelin staining include area MT (Van Essen et al., '81; Gattass and Gross, '81; Ungerleider and Mishkin, '79; Ungerleider and Desimone, '86a; Fig. 3); area V3d and V3v (VP) (Van Essen, '85; Burkhalter et al. '86; Burkhalter and Van Essen '86; Ungerleider and Desimone, '86b; Colby et al., '88); and area PO (Colby et al., '88). The myeloarchitectural criteria of Ungerleider and Desimone ('86a) were used to describe area FST adjoining area MT anteriorly in the floor of the the superior temporal sulcus, and area V4t (Fig. 3), located on the lateral border of area MT. The myeloarchitectural criteria of Colby et al. ('88) were used to locate areas MIP and PIP. The cytoarchitectural criteria of Walker ('40) were used to parcell the frontal cortex, and those of Von Bonin and Bailey ('47) were used for areas LC and LA of the cingulate gyrus and areas TE, TF, and TH of the ventral temporal lobe.

Hierarchical ranking of cortical connections based on laminar distribution of labelling

Hierarchies that have been constructed at early levels in visual cortex have used the rule that feedforward projections are derived from cells located in the supragranular layers and terminate in the middle cortical layers (i.e., layers IV and III) (Rockland and Pandya, '79; Maunsell and Van Essen, '83). Feedback projections, on the other hand, are derived from supragranular and infragranular layers and
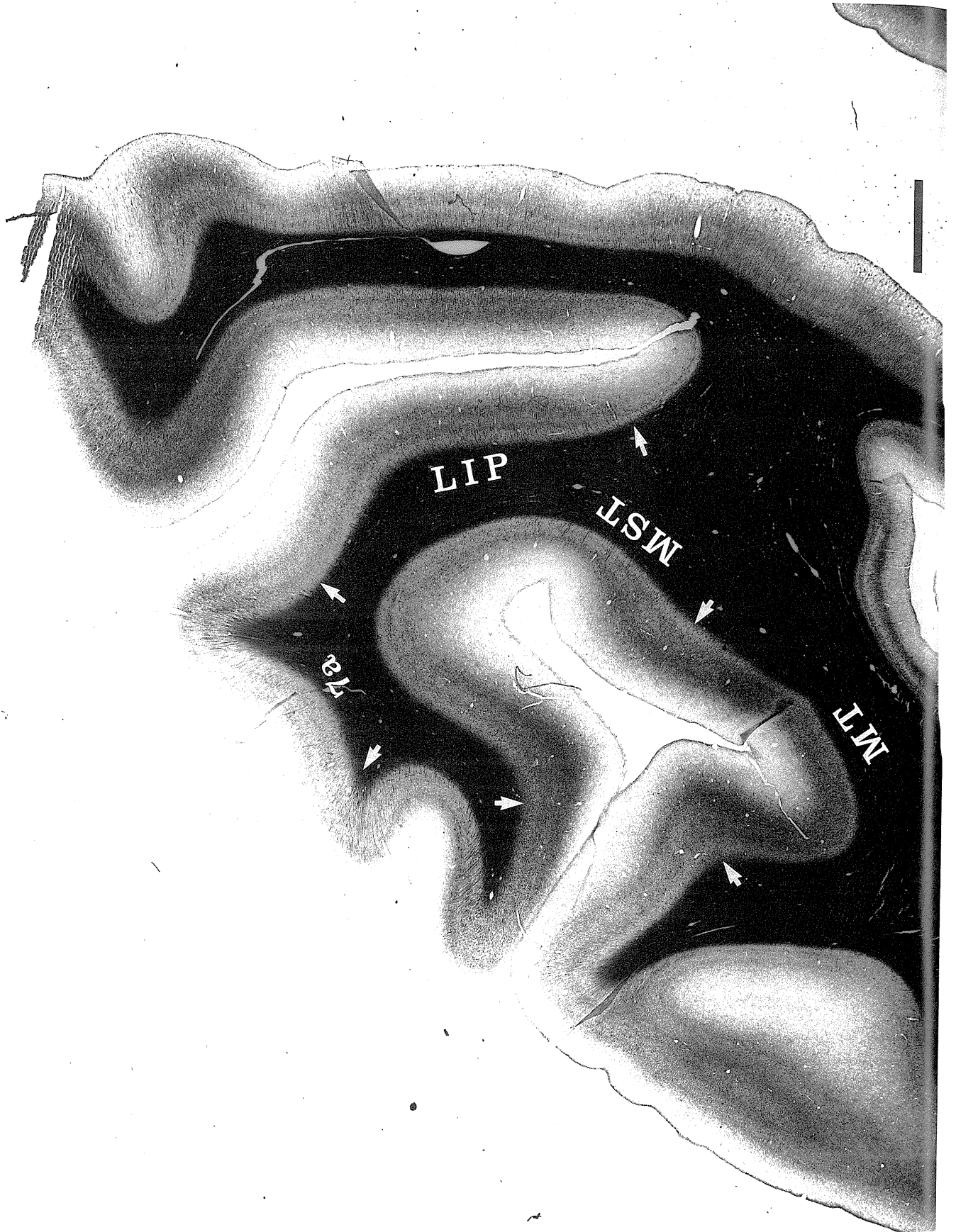
end in layers I and VI. We found it was possible to construct a hierarchy at the higher levels of the visual pathway if some aspects of these rules could be changed. The major change is that the feedforward projections are derived from both the supragranular and infragranular layers. The results presented below indicate that, in general, all projections of the cortical regions studied were derived from cells in layers III, V, and VI. Thus the disposition of the anterograde terminal labelling became the primary determinant of the positions of cortical fields within the hierarchy.

We shared the assumption of Maunsell and Van Essen ('83) and Ungerleider and Desimone ('86b), that if the terminal labelling was found to be fairly evenly distributed in all cortical layers, such a projection was to be considered intermediate, indicating that the two cortical fields were at approximately the same level in the hierarchy. We noted, as had Ungerleider and Desimone ('86b), that for some cortical fields there is a patchy pattern of efferent labelling with some patches demonstrating feedforward patterns and other patches feedback patterns. We have named this pattern of labelling "mixed" to distinguish it from a more continuous density of labelling in all layers, for which we retained the name "intermediate." In constructing the hierarchy, we have interpreted that either mixed or intermediate labelling patterns indicates that the two connected areas are on approximately the same level. Similar rules for hierarchical ranking have also been applied to the somatosensory system (Friedman, '83) and thus are also extended to projections involving somatosensory areas in this study.

RESULTS
Area 7a

In total 12 separate connectional studies were made of area 7a, 5 using anterogradely transported tritiated amino acids and the remainder retrogradely transported fluorescent dyes. Below is a description of the ipsilateral projections. Comparison of the anterograde and retrograde experiments indicated that all area 7a neocortical connections are reciprocal.

Temporal lobe. Area 7a projects extensively to two regions in the temporal lobe, the cortex of the superior temporal sulcus (STS) and the parahippocampal gyrus. Within the STS area 7a projects largely to the anterior bank of the sulcus, including areas MST and the superior temporal polysensory area (STP, Bruce et al., '81) (Figs. 4, 5, 8, 10). However, there is also extensive label in the floor of the sulcus in area FST and in the most rostral aspect of the sulcus (Figs. 5, 8, 10). This latter region is within the inferotemporal cortex (area TE) and likely corresponds to cortex where, among other properties, neurons selective to faces have been found (Perrett et al., '82; Desimone et al., '84). Some label is also found on the posterior bank of the rostral third of the sulcus (Fig. 5), again clearly within the inferotemporal cortex. This projection is important, since it represents the only direct connection between the posterior parietal cortex and the inferotemporal cortex. In no case in which sections were stained for myelin was labelling found

in the heavily myelinated aspect of the caudal posterior bank of STS that corresponds to area MT (Fig. 10).

The anterograde terminal labelling was densest in layers I, V, and VI of area MST, although labelling was also seen in the other layers. Area STP terminal labelling was often patchy with labelling in all layers. Some patches had higher concentrations of label in layers III and IV, and others had higher concentrations in layers I and VI. The retrogradely labelled neurons were found in high numbers in layers III, V, and VI in all areas of the STS projecting to area 7a. These results suggest that area MST feeds forward to area 7a. The pattern of labelling in area STP suggests that some patches of STP are located at a level above area 7a in the cortical hierarchy, whereas other patches are located at a level below area 7a. A similar pattern of labelling was noted by Ungerleider and Desimone ('86b) for the projections of area MT to area V4. We refer to this pattern of labelling as *mixed,* containing distinct patches of feedforward and feedback patterns.

Figure 10 shows a direct comparison of the ipsilateral associational connections of area 7a and prefrontal cortex with the superior temporal sulcus. In this case multiple injections of NY were made in the frontal eye fields (FEF) and area 46 of Walker in the frontal lobe, and several large injections of FB were made centered in area 7a. Note that the prefrontal regions receive input from virtually the entire sulcus, whereas the area 7a projection, although extensive, originates from a more restricted extent of the sulcus. The projection to the frontal lobe is discontinuous in strength and originates from layers III, V, and VI. Several areas of STS project to both the prefrontal cortex and area 7a and there is no clear systematic organization of the relative waxing and waning of the two projection populations. In other words, the dense regions (or sparse areas) of the two projections do not appear to either interdigitate or completely overlap; rather the pattern appears to be one of partial overlap with no obvious systematic structure. The callosal connections of these two areas with the contralateral STS were similar to the ipsilateral pattern, only a little weaker. Less than 1% of the neurons were found to be double-labelled in these experiments.

The projection from area 7a goes to two regions within area TF of the parahippocampal gyrus that can be distinguished by differences in the laminar pattern of the retrogradely labelled neurons (Fig. 5). The one region is located more laterally and posteriorly on the gyrus with labeled neurons in layers III, V, and VI. The second cortical area is located medially and anteriorly on the gyrus, and its projection to area 7a originates predominantly from layer VI. Efferent terminal label from area 7a ends in the more lateral cortical area (TFl) predominantly in layers VI and IV. The more medial area (TFm) has the highest concentration of terminal label in layer IV. These results suggest that the medial field receives feedforward projections from area 7a and the lateral field provides feedforward projection to area 7a. A projection from area 7a to the presubiculum was also observed that was not reciprocal. This result confirms the projection from area PG to the presubiculum reported by Seltzer and Van Hoesen ('79).

Occasional cells were seen on the lateral aspect of the inferior temporal gyrus in areas TEO and TE. This projection was more prominent with area LIP injections and may reflect slight tracer spillage at the injection site into this region. Although very few cells were observed, the ones that were labelled often were the most intensely labelled of any

Fig. 3. Myelin-stained coronal section through the posterior parietal cortex showing borders of areas MT, LIP, 7a, and MST based on myeloarchitecture. The densely myelinated zone (DMZ) is located within area MST and marks the dorsal border of MST.
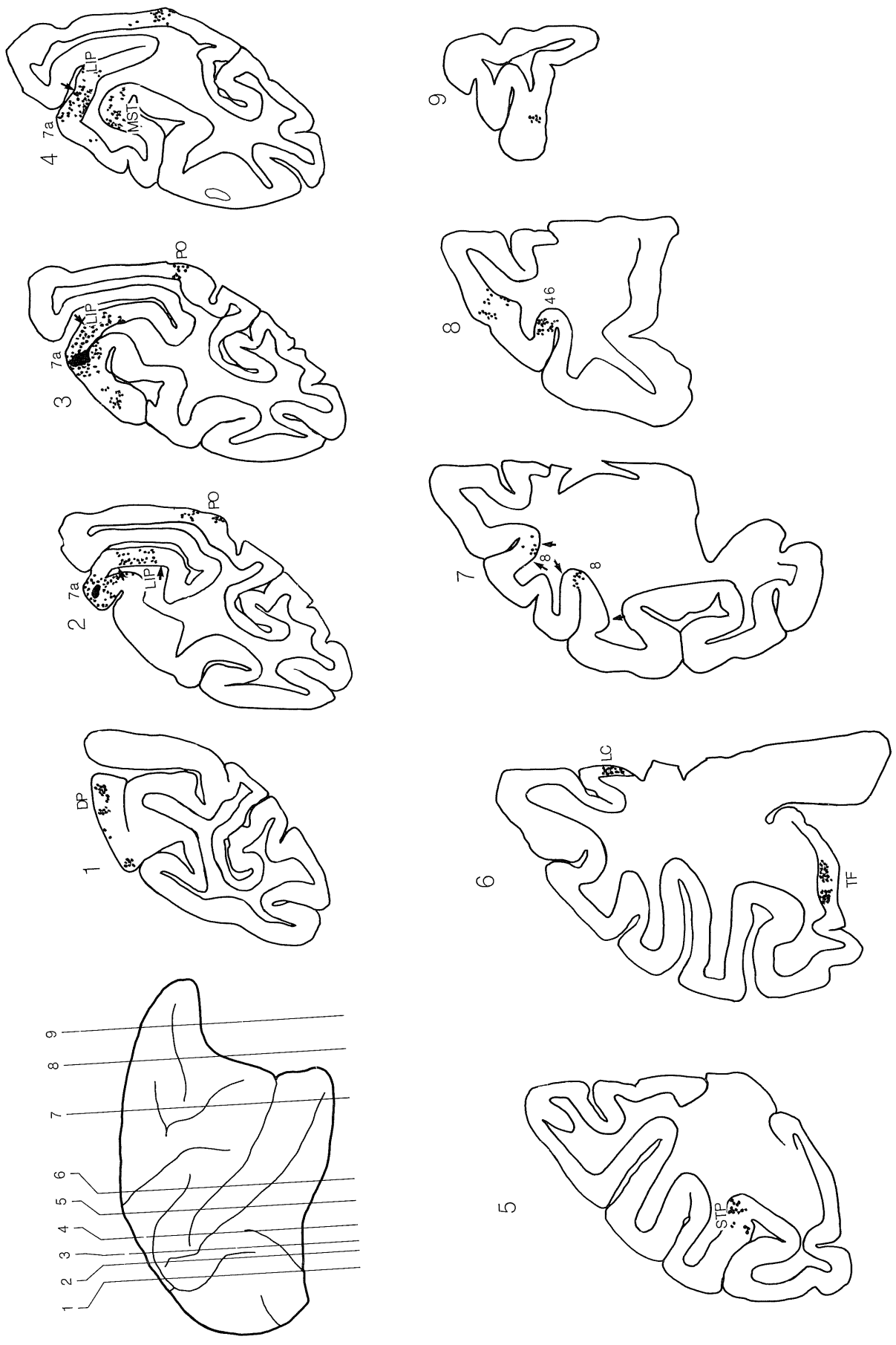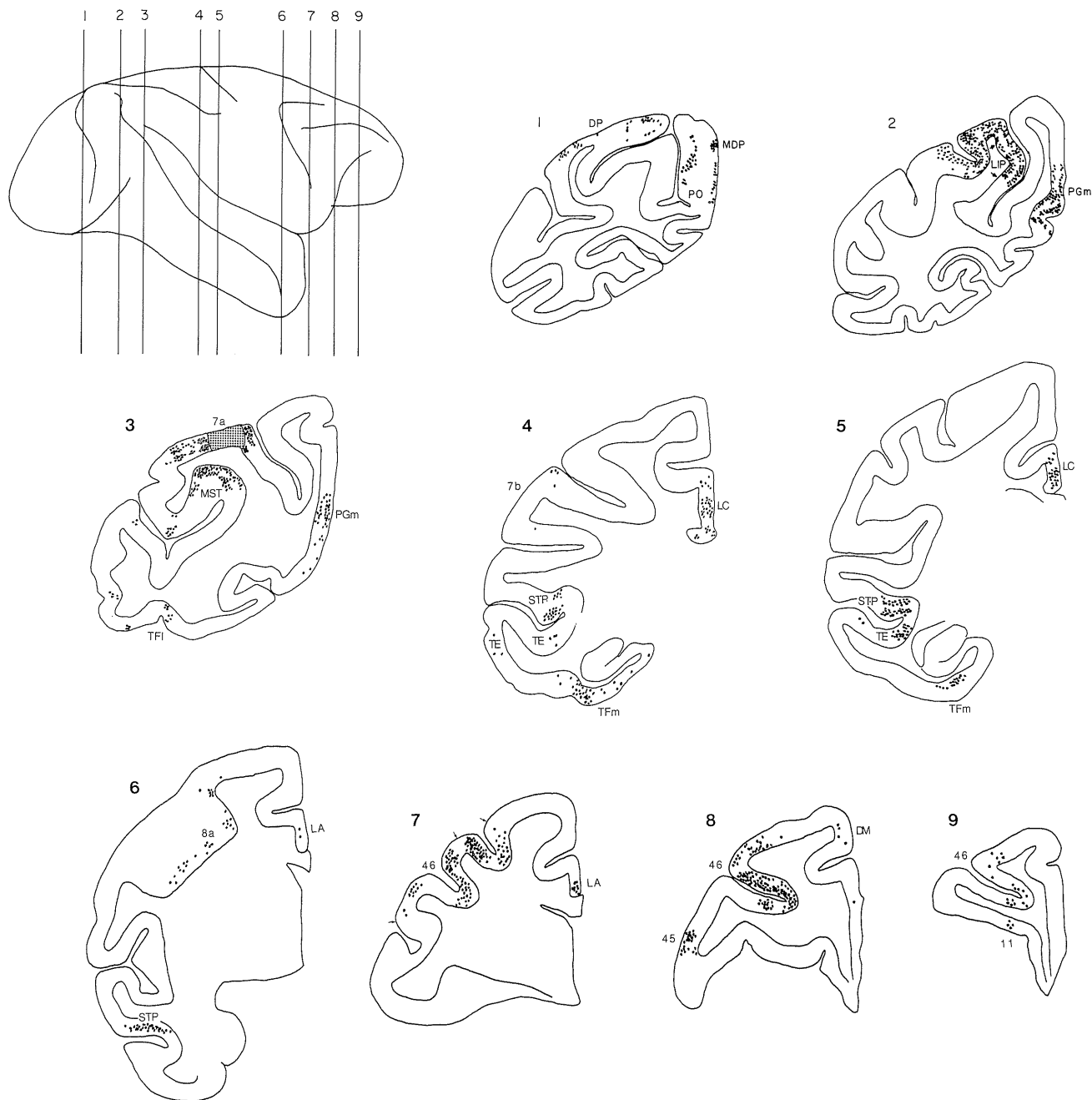
Figure 4

Fig. 5. Labelling resulting from three closely spaced .5 μl injections of fast blue made in area 7a of the left hemisphere of case 5.

seen in these experiments with their dendritic processes being almost completely filled with dye.

Parietal cortex. Label was extensive over a large area of the posterior parietal cortex. Strong connections were found with both the heavily myelinated and lightly myeli-

Fig. 4. Pattern of label in coronal sections from the left hemisphere after a .05 μl injection of fast blue into area 7a of the left hemisphere of case 15. Unless otherwise indicated, all labelled sections are from the same hemisphere in which the injection was made.

nated aspects of area LIP (Figs. 2, 5, 8). The retrograde labelling experiments indicated that the LIP to 7a projection arises from pyramidal cells from layers III, V, and VI, whereas the anterograde tracing experiments showed strongest terminal labelling in layer I followed by layers V and VI followed by layers II, III, and IV. This pattern of projection suggests that area LIP is lower in the cortical hierarchy and is a possible source of visual input to area 7a.

A new projection of considerable importance was found as a pathway for visual input into area 7a. The projection originates from area DP in the dorsal aspect of the prelunate

gyrus dorsal to area V4 and projects to area 7a (Figs. 4–8). Our recording experiments confirm the observations of Maguire and Baizer ('84) that this area is made up of visually responsive neurons with large receptive fields. This projection probably was missed in earlier tracing experiments of area 7 since large injections were used which often led to involvement of this area in the injection site. However, the label recorded in the present experiments cannot be a result of tracer diffusion outside of area 7a, since even when very small (.05 μl) injections were made into area 7a with no spillage of tracer into DP (Fig. 4), there was still extensive labelling in DP. Also, small injections (.05 μl) of anterograde and retrograde tracer into DP led to labelling in area 7a (see next section). The projection from DP to 7a originates in layers III, V, and VI (Fig. 7). The projection from area 7a to DP ends in terminals concentrated most heavily in layers I and V followed by layer VI and with the lightest labelling in layers II and III. These patterns of source and terminal labelling suggest that DP feeds forward to area 7a and that area 7a feeds back to DP.

Extensive anterograde and retrograde labelling was also noted in the parieto-occipital area PO after area 7a injections (Figs. 4–6, 9). Although labelling was found throughout PO, it also extended to regions outside PO, including the medial intraparietal area (MIP), posterior intraparietal area (PIP), and medial dorsal parietal area (MDP) of Colby et al. ('88) (Fig. 4). The label on the medial wall of the hemisphere continued anteriorly through areas PGm of Pandya and Seltzer ('82) and merged with label in area LC of Von Bonin and Bailey ('47) in the cingulate gyrus (Fig. 4). Thus there is a continuous area of labelling that begins in area PO and extends anteriorly on the medial wall of the hemisphere into the cingulate gyrus. Projections from these various areas to area 7a all originated in layers III, V, and VI (Fig. 9). The efferents from 7a to PO ended predominantly in layer VI followed by V, with sparse labelling in the other layers. Thus the connections from PO to area 7a appear to be of the feedforward type and from 7a to PO of the feedback type. The connection with area PO represents another possible source of visual input from areas of extrastriate cortex lower in the hierarchy to area 7a. The connections of area PGm with 7a are of the intermediate type and are interpreted as indicating that the areas 7a and PGm occupy a similar level in the cortical hierarchy.

Although label was found in area 7b after area 7a injections (Figs. 4, 8), it was usually only seen with large injections or injections in which tracer at the injection site might have diffused into area 7b. Thus, it is unclear whether areas 7a and 7b are connected, but if they are the connection does not appear to be a strong one. In some cases where label was found in area 7b, labelling was not seen in areas connected to 7b, suggesting that connections between areas 7a and 7b do exist. No projection was found to area 5.

Frontal lobe. Area 7a connects to areas 46 (prefrontal), 8a (frontal eye fields), and 45 of Walker ('40) in the frontal lobe (Figs. 4, 5, 19). The connection with area 46 is the strongest of the three with area 7a injections. This result is in contrast to area LIP, which connects most strongly to the frontal eye fields, and area 7b, which connects most strongly to area 45 (Fig. 19). The reciprocal connections of area 46 with area 7a derive from both banks and the fundus of the principal sulcus, although they are strongest from the dorsal bank (see also Andersen et al., '85a). The projections from the frontal lobe arise from layers III, V, and VI. Area 7a efferents end in layers III and II in area 8a. Thus area 7a

appears to feed information forward to the frontal eye fields. Weak projections to the supplementary eye fields (SEF) of Schlag and Schlag-Ray ('86) anterior to area 6, and a weak projection to area 11 of Walker ('40) in the orbital cortex of the frontal lobe were also found (Fig. 5, section 9).

Cingulate cortex. Area 7a has extensive connections with the cingulate gyrus (Figs. 4, 5, 11). The most interesting aspect of this projection is that it is of similar strength ipsilaterally and contralaterally, whereas the other callosal connections of area 7a are weaker than the ipsilateral connections (Fig. 11). This projection is stronger with the posterior aspect of the gyrus (area LC) compared to the anterior aspect (area LA). The retrogradely labelled cells were found in layers III, V, and VI, and terminal labelling was found in all layers at about equal strength. This intermediate laminar pattern of labelling suggests that the cingulate gyrus is located at the same level as area 7a in the cortical hierarchy.

Callosal connections. In cases where single small injections of tracer were made into area 7a, label was seen in contralateral areas 7a, DP, PO, LIP, MST, PGm, LC, LA, and STP. With large and multiple injections of fluorescent dyes into area 7a, fairly extensive labelling was also seen contralaterally in areas MIP, MDP, and PIP and occasional labelled neurons were seen in TEO, IT, TFl, and TFm.

The dorsal prelunate area (DP)

The finding, with area 7a injections, of a projection from the dorsal aspect of the prelunate gyrus to area 7a was of great importance since this pathway represents a major source of visual inputs into area 7a. In light of this discovery, and the lack of any previous anatomical studies of this region of the brain, we decided to examine the overall connections of area DP. Three experiments were performed in area DP, two using anterograde tracers and one using retrograde tracers. Area DP was found to receive inputs from extrastriate visual cortex (V3A, PO, and V4), and to project to several visual areas within the posterior parietal cortex (MST, LIP, and 7a) (Figs. 12–15). All corticocortical connections were found to be reciprocal, with one exception. Anterograde label was seen in area 8a but not retrograde label; however, even the anterograde labelling was very weak and raises the possibility that a weak reciprocal connection exists, but the one retrograde tracing case was not sensitive enough to show it.

Ascending visual inputs. Area DP receives inputs from areas V4 and V3A that are judged to be ascending in the cortical hierarchy based on the pattern of laminar labelling (Figs. 12–15). Both regions send projections to DP from cells located in layers III, V, and VI. The efferent labelling is of the feedback style for both areas being concentrated in layers I and VI. Area V4 also showed lighter labelling in layers II and V and slight labelling in layer IV. Area V3A had lighter labelling in layers III, IV and V. The projection from area PO was of the intermediate type with source cells being located in layers III, V, and VI and labelled terminals in all layers (Figs. 12, 15). The labelling in PO was very faint in these experiments.

Projections into the inferior parietal lobule. The dorsal prelunate area projects extensively to areas 7a, LIP, and MST (Figs. 12–15) of the posterior parietal cortex. All of these areas are exclusively or predominantly visual cortical fields. Area DP was not found to project to area 7b, a predominantly somatosensory area. Label was also not found in area VIP. Retrogradely labeled cells were found in
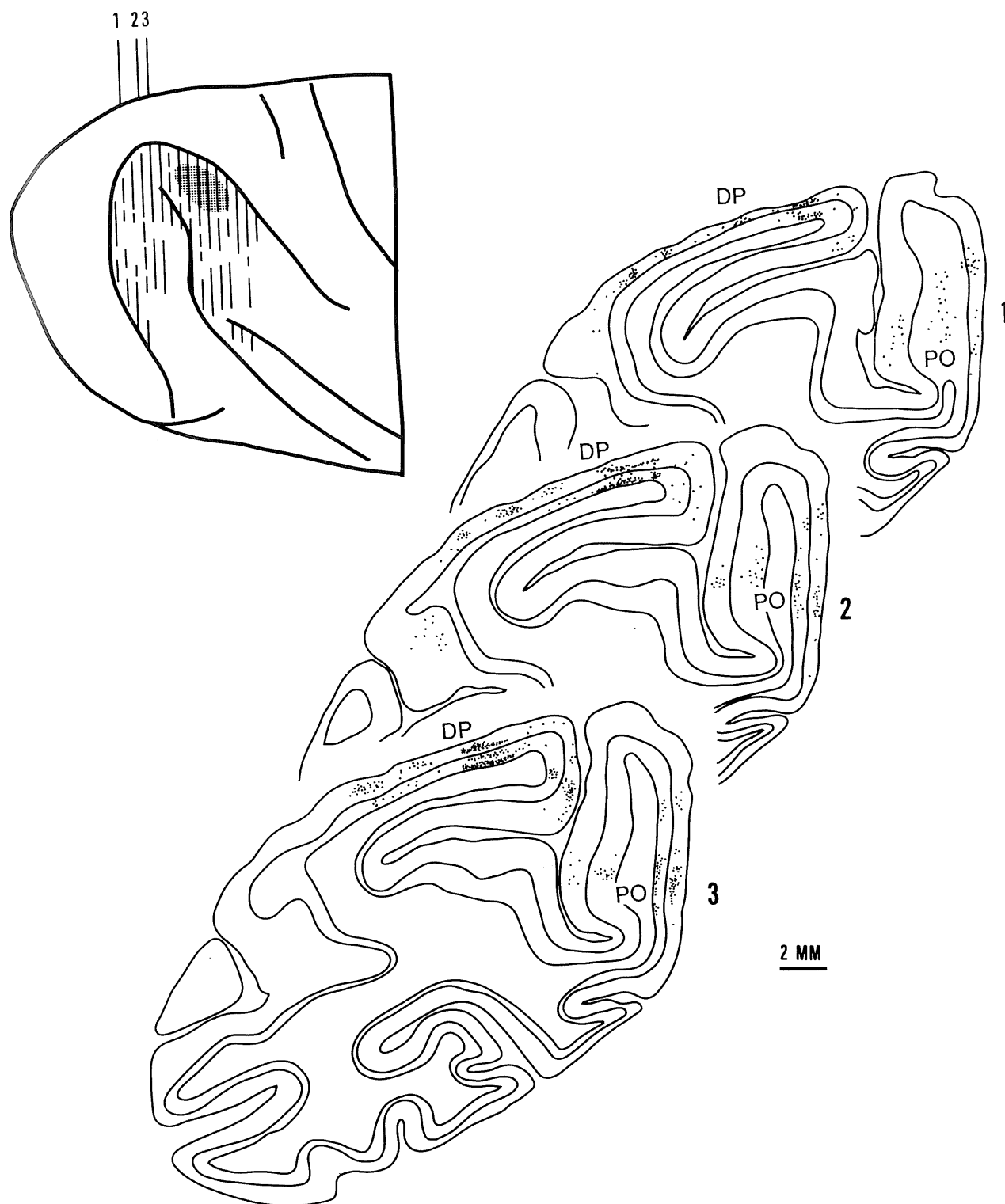
Fig. 6.   Labelling in area DP after area 7a injections. The **upper left inset** shows the posterior half of the hemisphere of case 5. The stippled area indicates the extent of the fast blue injection site. The dark stripes show areas of local labelling recorded from the coronal sections. Three of these sections are shown on the right.
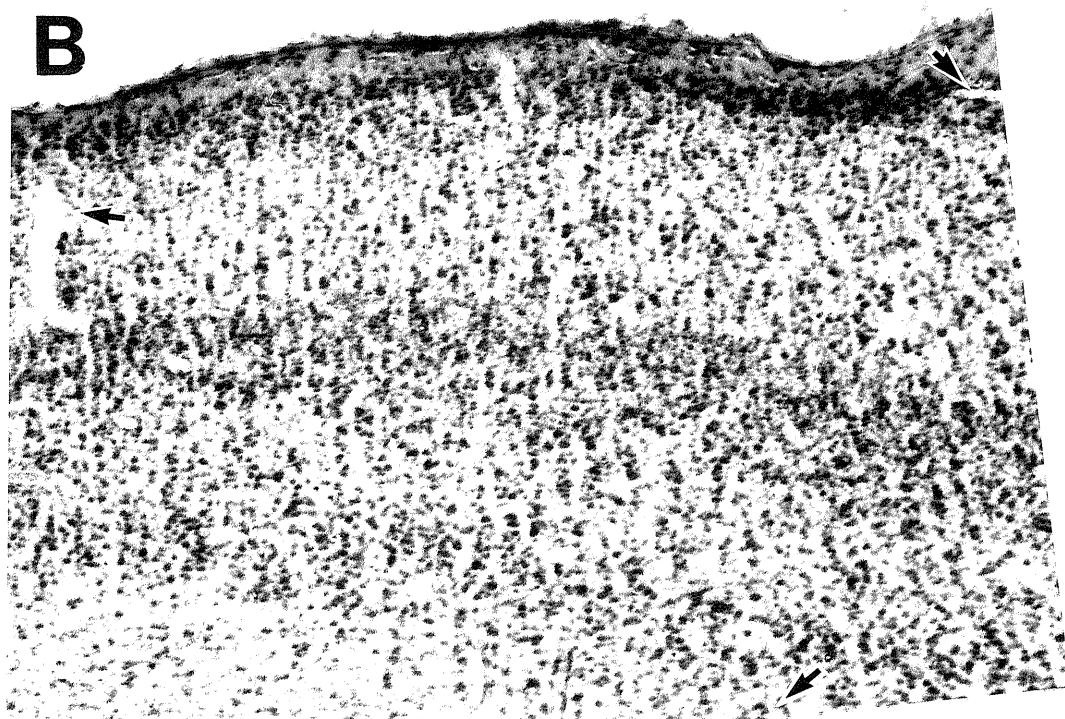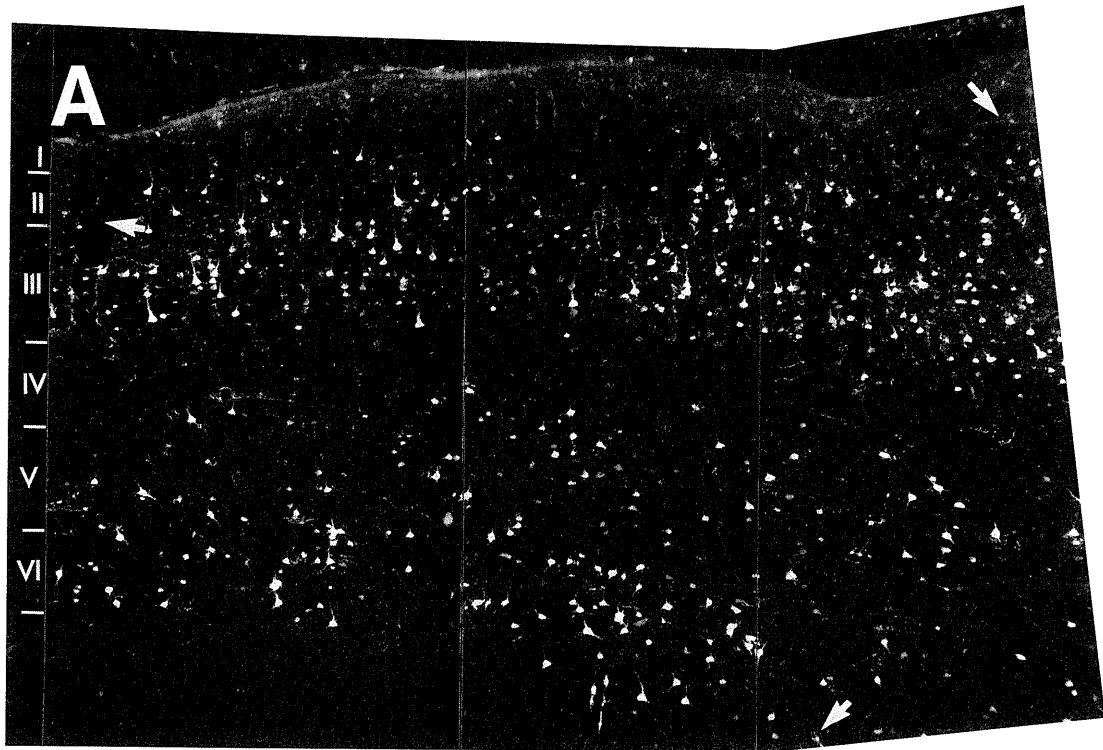
Fig. 7.   Laminar pattern of labelling in area DP after area 7a injections of fast blue in the left hemisphere of case 8. **A:** Fluorescence photomicrograph through area DP. **B:** Adjacent Nissl stained section to the section in A. Note that cells projecting from area 7a arise from layers III, V, and VI. Arrows indicate blood vessel landmarks that were present in both sections and were used to align these adjacent sections.

layers III, V, and VI in LIP, MST, and 7a after injections in area DP. Terminal labelling in area 7a was typical of the feedforward pattern with heavy labelling in layer IV, followed by layer III, and with very light labelling in layers VI and II. Labelling in area LIP was complex with some patches appearing feedforward (layer IV followed by layer VI and weaker labelling in the other layers) and some patches being of the intermediate type with rather uniform labelling in all layers. Overall the pattern of terminal labelling for area LIP was judged to be of the intermediate type. Terminal labelling in area MST was very weak, and it was difficult to determine the relative strengths of labelling in the various layers. These observations are consistent with the idea that area DP is a major source of visual input to the posterior parietal cortex.

In one case where multiple large injections of anterograde tracer were made into DP terminal label was also found in FST and VIP. Labelling in FST was concentrated in layer IV, indicating a feedforward projection, and VIP labelling was strongest in layers IV and VI with substantial labelling also in layers I–III and V, suggesting an intermediate pattern. Since the injection site was large and as a result also included the dorsal most aspects of area V4, these connections of area DP must be considered tentative.

Frontal lobe projections. Area DP projects to the prefrontal cortex. Retrograde labelling was found in both areas 8a and 46, and weak anterograde labelling was found in area 46. The terminal labelling was found predominantly in layers IV and III with weaker labelling in layers V and VI for area 46. This pattern of label suggests that area DP feeds forward to area 46.

Area LIP

Three experiments were performed in area LIP, two using retrograde tracers and one using anterograde tracer. In all three cases, injections were made with a syringe that was lowered through area 7a and into area LIP. In the case of the two retrograde tracing experiments, some tracer diffused up the needle track into area 7a and resulted in labelling indicative of both area 7a and area LIP. In the anterograde tracing experiment, no labelling was seen along the needle track in area 7a, and the pattern of labelling was distinctly different from that found with 7a injections. In a subsequent set of experiments, we have made anterograde and retrograde tracer injections into area LIP using an anterior approach in which the needle is lowered through the superior parietal lobule (area 5), through the medial bank of the intraparietal sulcus, and into area LIP (Blatt et al., '87). The labelling from these injections was similar to that seen with the one anterograde tracer injection described in the present series of experiments and will be described in a subsequent publication.

Extrastriate cortex. The injection of tritiated amino acids into area LIP produced label in a large number of extrastriate cortical areas including areas MT, MST, DP, PO, 7a, V4, V3A, V3d, V3v, and TEO (Fig. 16). Terminal labelling in areas MT and V4 was of the feedback pattern, being confined primarily to layers I and VI. Terminal labelling in V3A was densest in layers V and VI and I and II and in V3v was densest in V, VI, and I. These feedback patterns of terminal labelling suggest that area LIP is higher in the visual hierarchy and receives visual inputs from these regions.

Labelling in area DP was strongest in layers IV and VI in some sections and strongest in layers I and VI in other

sections; but there was also substantial labelling in other layers, and thus the pattern appeared to be of the intermediate type. Label in area PO was dense in and around layer IV, but was also substantial in the other layers, suggesting an intermediate pattern. In area TEO in some sections labelling was strongest to layer III followed by layers I and II, followed by layer IV. However, in other sections label was evenly distributed over all layers suggesting that the area TEO is mixed. These results indicate that areas PO, DP, and TEO are at a similar level in the cortical hierarchy with area LIP.

Area MST had its densest labelling in layer IV followed by I, III, and VI, respectively. Area 7a was most densely labelled in layers IV and IIIb, followed by I followed by II and IIIa. These patterns of label are consistent with a feedforward pattern and suggest that areas 7a and MST lie above area LIP in the cortical hierarchy.

There was also terminal label found in area TF of the parahippocampal gyrus and in the frontal lobe (Fig. 19). The label in area TF was of the intermediate type, being strongest in layers IV and VI followed by layers V and II, followed by layer III. The label in the frontal lobe was in areas 46 and area 8a. The label in area 8a was much stronger and therefore represents the reverse of what was seen for area 7a injections, which produced heavier labelling in area 46 compared to area 8a (Fig. 19). The label in frontal lobe was of the feedforward type. Area 8a showed strongest labelling in layers IIIb and IV followed by I and II, followed by V and VI. Area 46 had the densest labelling in layers III–V and lighter labelling in layer I.

It should be noted that unlike area 7a, label was not found in anterior aspects of the superior temporal sulcus, the presubiculum, PGm, or in the cingulate gyrus.

Area 7b

The connections of area 7b involve a very different set of cortical areas than those of area 7a, DP, and LIP. In general, area 7b has connections with cortical areas known to have somatosensory functions, whereas the other areas investigated in this paper entertain connections with mostly visual areas. However, area 7b also has connections with some visual areas. Three successful experiments were performed in area 7b, two using anterograde tracers and one using a retrograde tracer. The corticocortical connections were all reciprocal.

Parietal and parieto-occipital connections. Anterograde and retrograde labelling was found in area 5 of the superior parietal lobule (Figs. 17, 18). In the one retrograde labelling experiment label was found in the medial aspect of the hemisphere in area PGm, in area PO, and in cortex dorsal to PO (area MDP of Colby et al., '88) (Fig. 17). In this case the label on the medial aspect of the hemisphere was continuous from PO to area 5. However, label in PO, PGm, and MDP was not found in the anterograde tracing experiments and in the one retrograde case there was slight spilling of tracer into area 7a (see Fig. 8); thus, it is possible that the labelling in PGm, MDP, and PO resulted from involvement of area 7a.

Label in area 5 for the anterograde and retrograde cases included both the gyral surface of the superior parietal lobule and the cortex in the medial bank of the intraparietal sulcus. In one case (Fig. 18) label was also found in SI and SII; however, the injection site included some of area SII (label was found in the ventral posterior inferior nucleus of the thalamus) and it is likely that this diffusion of tracer
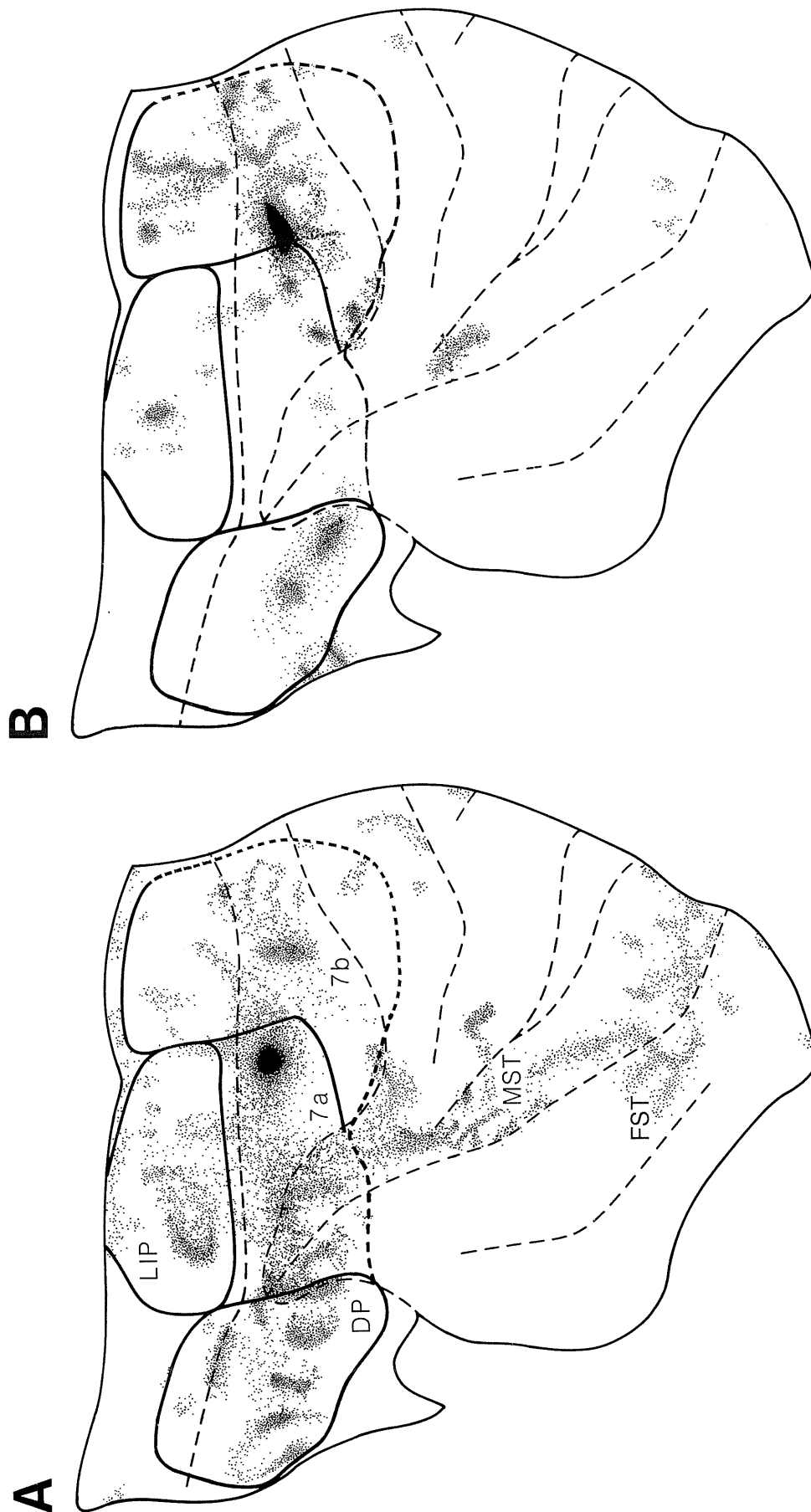
Fig. 8. Flattened reconstructions of the inferior parietal lobule of the left hemisphere of case 10 showing the pattern of labelling after two fluorescent dye injections. **A:** A single .5 μl nuclear yellow injection was made into area 7a. **B:** A single .5 μl injection of fast blue was made into area 7b, but a minority of the injection site also involved area 7a. This case allows a comparison of the two patterns of labelling in the same hemisphere.
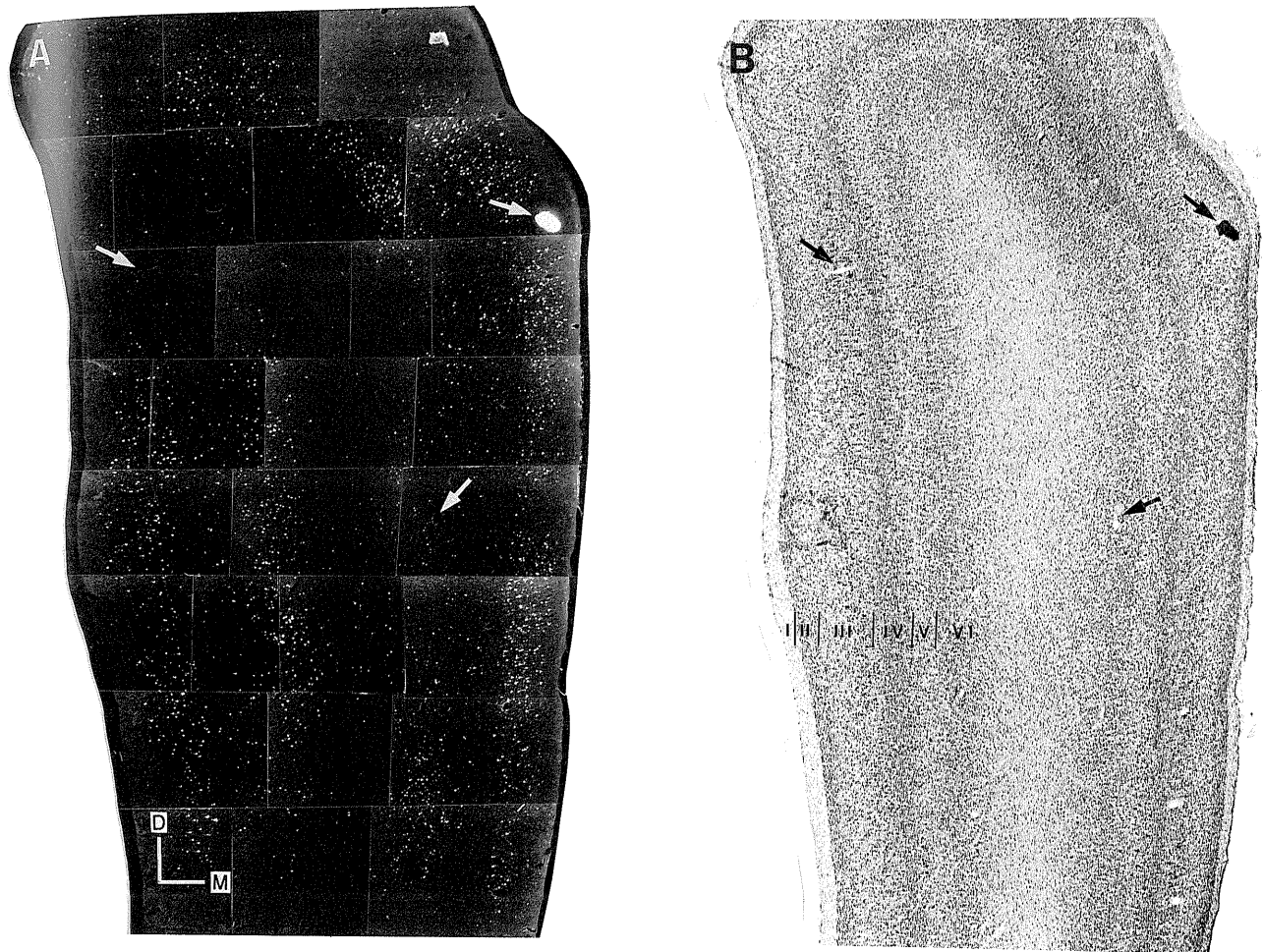
Fig. 9. Label in the medial wall of the occipitotemporal sulcus and medial wall of the left hemisphere of case 8 after injection of fast blue into area 7a. **A:** Fluorescence photomicrograph showing pattern of labelled cell bodies. **B:** The same section processed with a Nissl stain. The arrows indicate landmarks on the section that can be seen in both photographs. The layers of cortex are indicated in B. Note that labelled cells are found over a large area that includes area PO and adjacent regions. Labelled cells are located in layers III, V, and VI.

accounted for this additional labelling. In all cases there was label in the posterior and dorsal aspect of area MST and light labelling in area 7a (Figs. 17, 18), although again it is unclear if this is due to diffusion away from the injection site. One indication that this may not be a diffusion artifact is that none of the numerous visual areas known to connect to areas MST and 7a were labelled.

Retrograde labelling in all cortical areas was found in layers III, V, and VI. Anterograde labelling was strongest in layer VI followed by layer I, with some weak labelling in the remaining layers for area 5. Labelling in MST was strongest in layers VI and I, then V, then II and III. Both patterns of label are feedback and suggest that area 7b receives ascending somatosensory inputs from area 5.

Besides area MST, labelling was also seen in more rostral aspects of STS, including the anterior bank in area STP and the fundus in the region of area IT. Terminal labelling in area STP was of the mixed class with some patches having strong labelling in layers I and II followed by layer III with light labelling in the other layers, and some patches having strong labelling in layers III and IV followed by V and VI.

Labelling in IT was feedback being strongest in layer IV followed by layer VI.

Cingulate. There is extensive bilateral labelling of the cingulate gyrus (Figs. 11, 17, 18). However, unlike area 7a, which showed stronger connections to area LC in the posterior aspect of the gyrus, area 7b connects more strongly to area LA in the anterior aspect of the gyrus (Fig. 11). The anterograde labelling was rather evenly distributed over all layers, indicating an intermediate pattern.

Insular cortex. Area 7b has strong connections with area Ig of the insular cortex (Figs. 17, 18). Anterograde labelling is of the intermediate type, being distributed more or less uniformly throughout the radial dimension of the cortex.

Frontal lobe. Area 7b connects with the frontal lobe, but in a much different pattern than areas 7a, DP, or LIP (Fig. 19). Area 7b has very strong connections to area 45, and also connects to premotor cortex (area 6). Labelling in area 45 is of the feedforward type, primarily concentrated in layer III followed by layer V with weaker labelling in the other layers. In area 6 the pattern is also feedforward, with
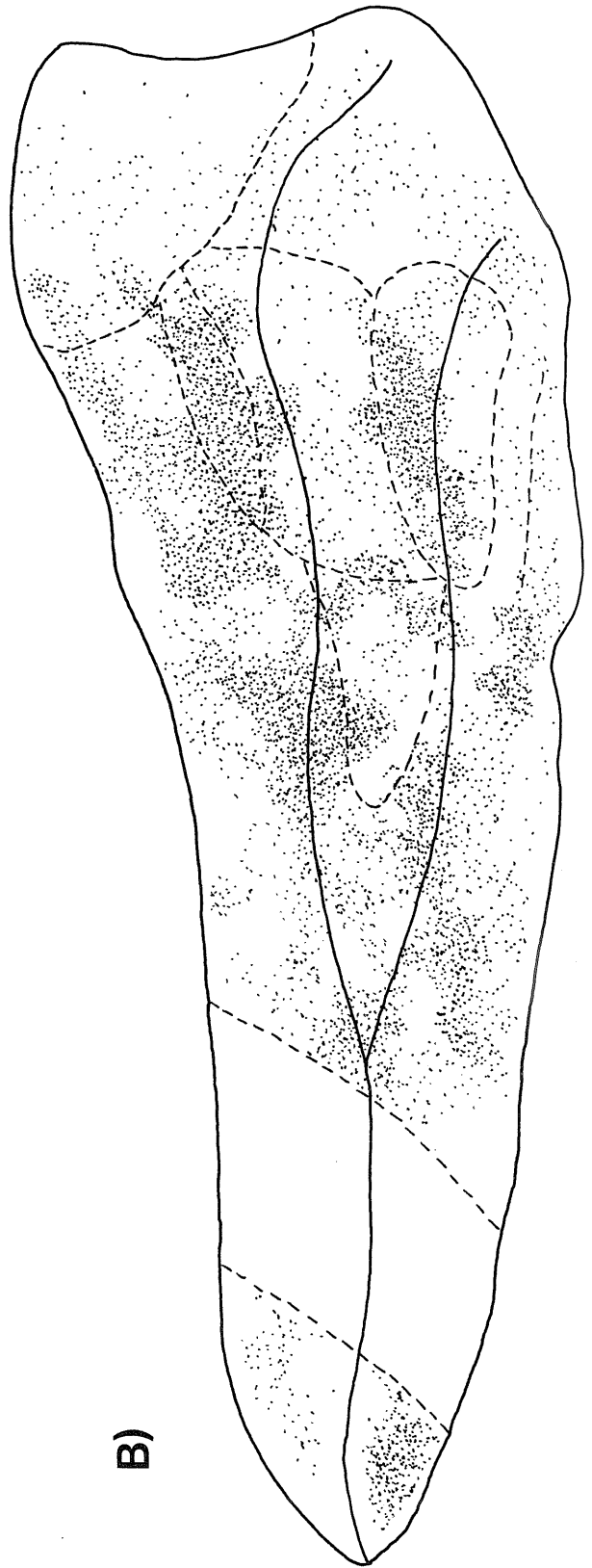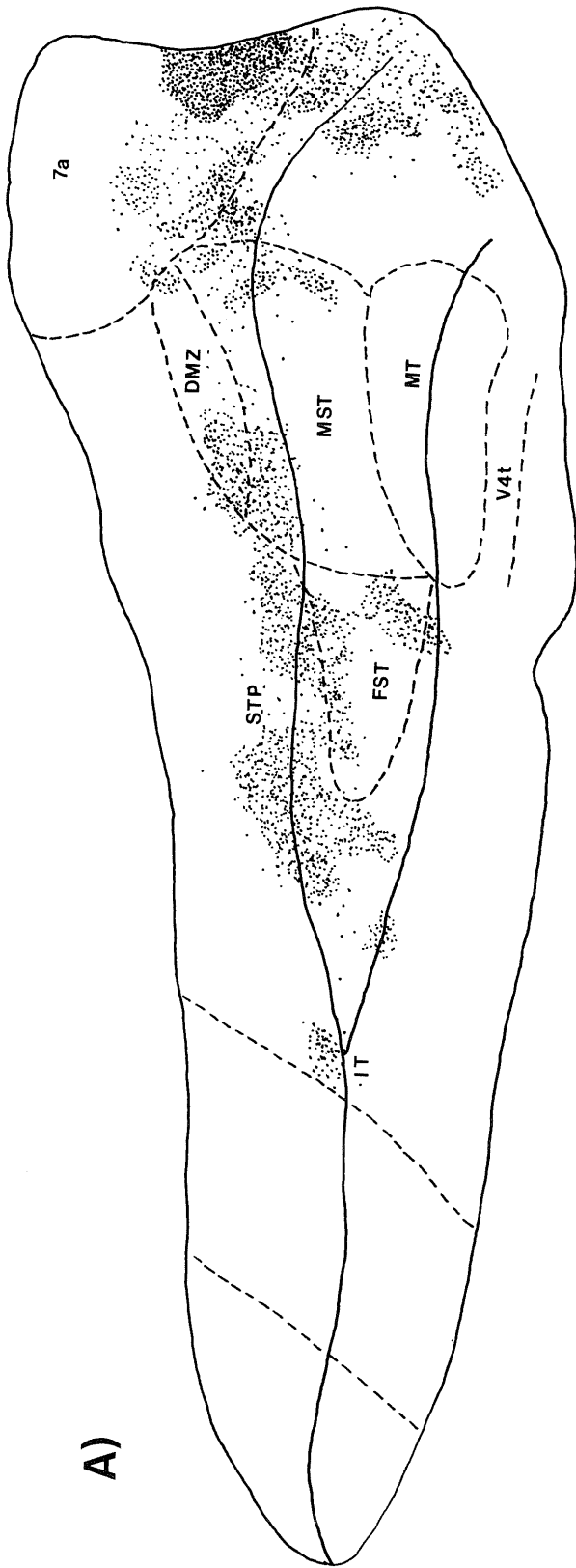
strongest labelling found in layers III and IV followed by layers V and then VI. A projection was also noted to area 12 of Walker in the orbital prefrontal cortex. Terminal labelling in area 12 was strongest in layer IV but with substantial label in layer VI as well.

Functional organization of the inferior parietal lobule

In three hemispheres of two animals the functional organization of the inferior parietal lobule was extensively mapped. These mapping experiments were performed in awake, behaving animals and required up to 4 months of daily recording per hemisphere. In two of the hemispheres, after the mapping was complete, single, small (.05 μl) injections of retrograde tracer were made in area 7a. Figure 1 shows these two injection sites. Thus the injections were made into cortical regions defined on functional as well as anatomical criteria.

Figure 20 shows a Nissl stained cross section through one of these hemispheres. The hollow arrow indicates the site of a .05 μl injection of Nuclear Yellow into area 7a. The dark arrow indicates a lesion made by passing current through a microelectrode at the end of a recording track in area LIP. Figure 1A shows a fluorescence micrograph of the injection site in this hemisphere. Figure 4 shows label after a .05 μl injection of fast blue into the left hemisphere of this animal; the injection site is shown in Figure 1b.

In the mapping experiments a very clear functional border between areas 7a and 7b was identified by a transition from visually sensitive cells to cells sensitive to somatosensory stimuli (Fig. 21A). Visual cells were recorded in areas 7a, LIP, and DP. In area 7b cells responded to cutaneous or deep somatic stimulation, and large numbers of them were sensitive to changes in joint angle. The somatosensory receptive fields were large and could cover an entire limb or, in rare cases, most of the body. Area 7b was easily distinguished from area 5 by the finding that area 7b cells receive bilateral input, whereas area 5 cells generally respond only to contralateral stimulation.

Quantitative analysis of the visual, saccade, and eye-position properties were performed on 408 cells located primarily in areas 7a and LIP. The distribution of these response properties for recording in areas 7a and LIP of one hemisphere is shown in Figure 21. In the following paragraphs, the functional properties of these two areas are compared.

Eye position. Three hundred fifty-seven of the total 408 neurons were tested for eye-position sensitivity in either the light or the dark or both. One hundred eighty-two of these cells (51%) showed a modulation of activity by eye position. Of these 182 neurons, 147 were also tested for light sensitivity and 94 (64%) were found to also respond to light. Figure 22 shows an example of a neuron showing both eye-position and light responses.

Several control experiments were performed to determine if the eye-position signal was of retinal or extra-retinal origin. A signal of retinal origin would result if the cells are responding to changes in the retinotopic pattern of the visual input resulting from changes in eye position. For instance, if the cell is visually responsive, at certain eye positions visual stimuli from the background of the lighted recording chamber might fall within the receptive field of the neuron, resulting in its activation, whereas at other eye positions there may be no visual stimulus in the receptive field and thus little or no activity. An eye-position signal of extra-retinal origin would be derived either from an efference copy of the motor output or from proprioceptive inputs from the extraocular muscles or orbital tissue.

Seventy-seven of the cells showing eye-position effects were tested in both the light and in total darkness. Only five of these cells had eye-position effects in the light but not in the dark. This result suggests that most of the eye-position effects are of extra-retinal origin since no background visual stimuli are present in the dark.

In another control the animal was trained to fixate a point of light at different gaze angles in otherwise total darkness and then to maintain fixation at that remembered location during a 1 second period in which the fixation point was turned off. Under these conditions the only possible source of an eye-position signal is extra-retinal since there are absolutely no visual stimuli present. Of 67 neurons demonstrating eye-position sensitivity, only 5 showed no eye position effects under these conditions.

In a final series of control experiments, the animal was trained to fixate a fixation spot in the *lighted* test chamber through prisms. By changing the diopter value of the prisms the animal was made to change eye positions without altering the retinotopic locations of the background stimuli. Eleven of twelve cells tested in this fashion were found not to change their eye-position tuning under these conditions.

The above experiments indicate that most eye-position effects for cells of the inferior parietal lobule are extra-retinal in origin.

Eye-position effects were found for cells in areas 7a, LIP, and DP (Fig. 21). We decided to examine more closely the properties of these eye-position effects to determine if there were any differences between areas 7a and LIP, the two areas from which we recorded the most data. Cells recorded at depths greater than 2.5 mm in the lateral bank of the intraparietal sulcus were considered to be in area LIP. The dorsalmost extent of the heavily myelinated portion of area LIP ended at approximately 4 mm deep in the intraparietal sulcus in all three hemispheres; however, the functional mapping experiments of Blatt et al. ('87) indicate that area LIP appears to extend 1–2 mm above the border of the densely myelinated portion. Eye position cells in area LIP were recorded from a depth of 2.5 mm to 11.9 mm with a mean depth of 4.74 mm, and 53% of the cells were within the heavily myelinated portion. No difference in eye-position sensitivity was seen between the cells in the heavily myelinated portion and the less myelinated region of area LIP located more dorsally.

In the experiments summarized above "gaze fields" of neurons were determined by having the animal fixate, at nine equally spaced eye positions, a small fixation point in otherwise total darkness. The fixation points were arranged on a 40° square grid centered on straight ahead fixation. The left panel of Figure 22 shows a "gaze field" determined in this way. Most of the gaze fields showed a monotonic

Fig. 10. Flattened reconstruction of the superior temporal sulcus of the left hemisphere of case 9. A: Fast blue labelling from multiple .5 μl injections of tracer in the ipsilateral area 7a. B: Nuclear yellow labelling after multiple injections of tracer in the ipsilateral prefrontal cortex in areas 8a and 46. Using two different retrograde labels in the same monkey affords a direct comparison of the populations of neurons in the superior parietal cortex projecting to area 7a in the posterior parietal cortex and to areas 8a and 46 in the prefrontal cortex. Dotted lines enclose the region of the superior temporal sulcus in which no sections were collected because the brain was blocked at this location.

a) Injection 7a

LC   LA

b) Injection 7b

5 mm

d

a
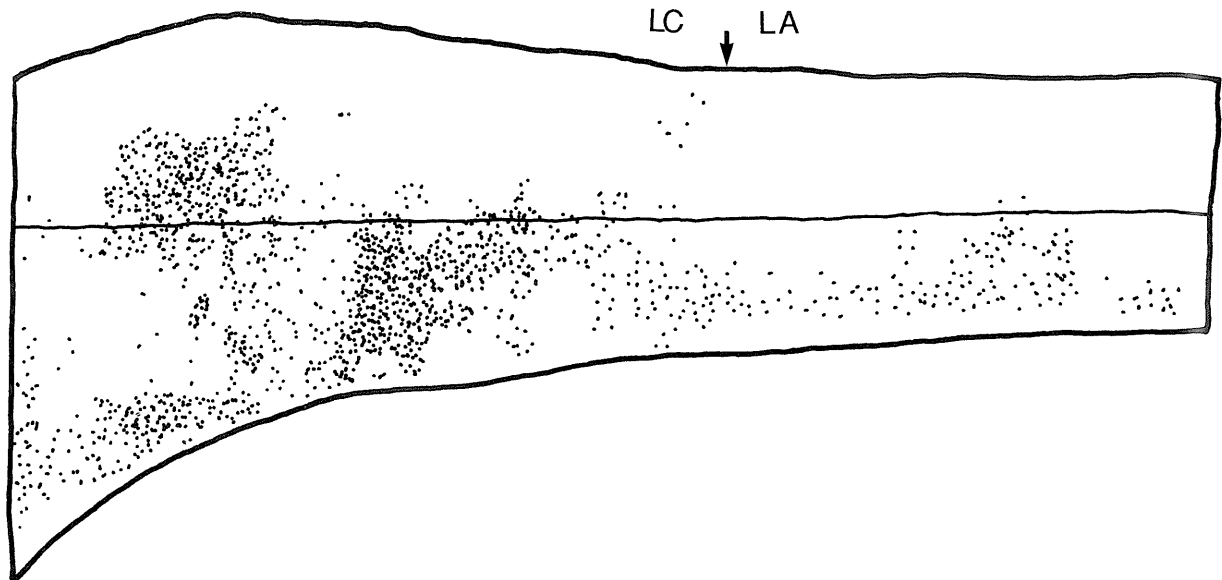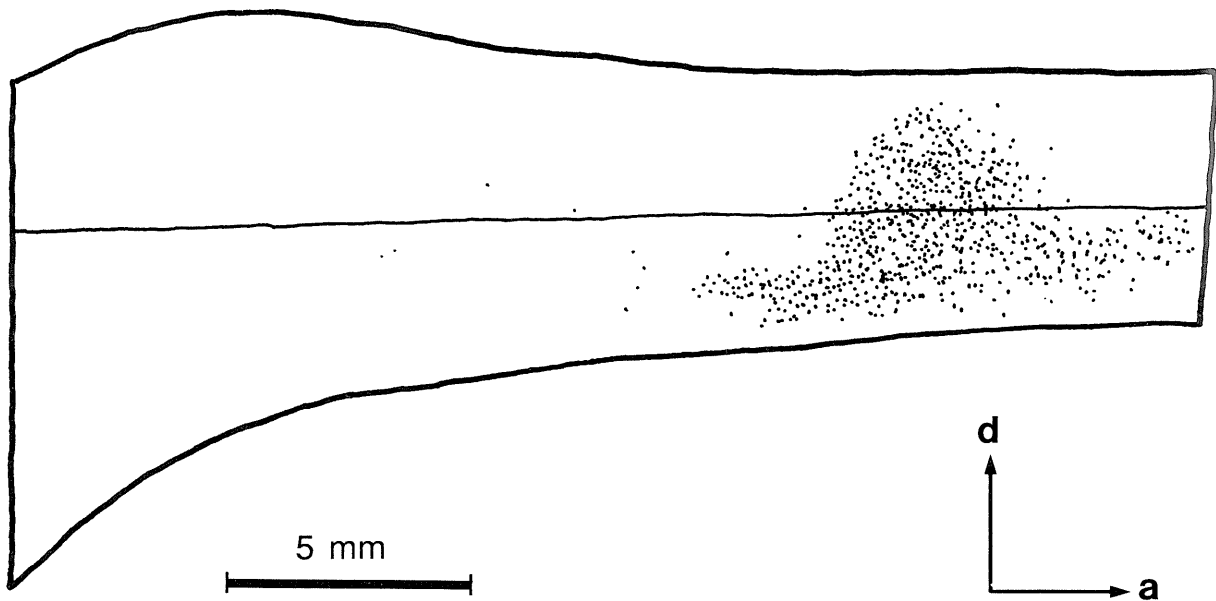
Fig. 11. Label in the left cingulate gyrus of case 10 after **a)** a .5 µl injection of NY into the left area 7a and **b)** a .5 µl injection of FB into the left area 7b. Anterior is to the right and dorsal is up. The arrow marks in panel a indicate the border between areas LC and LA. Note that 7a injections produce label concentrated more in LC, whereas 7b injections produce label concentrated more in LA.
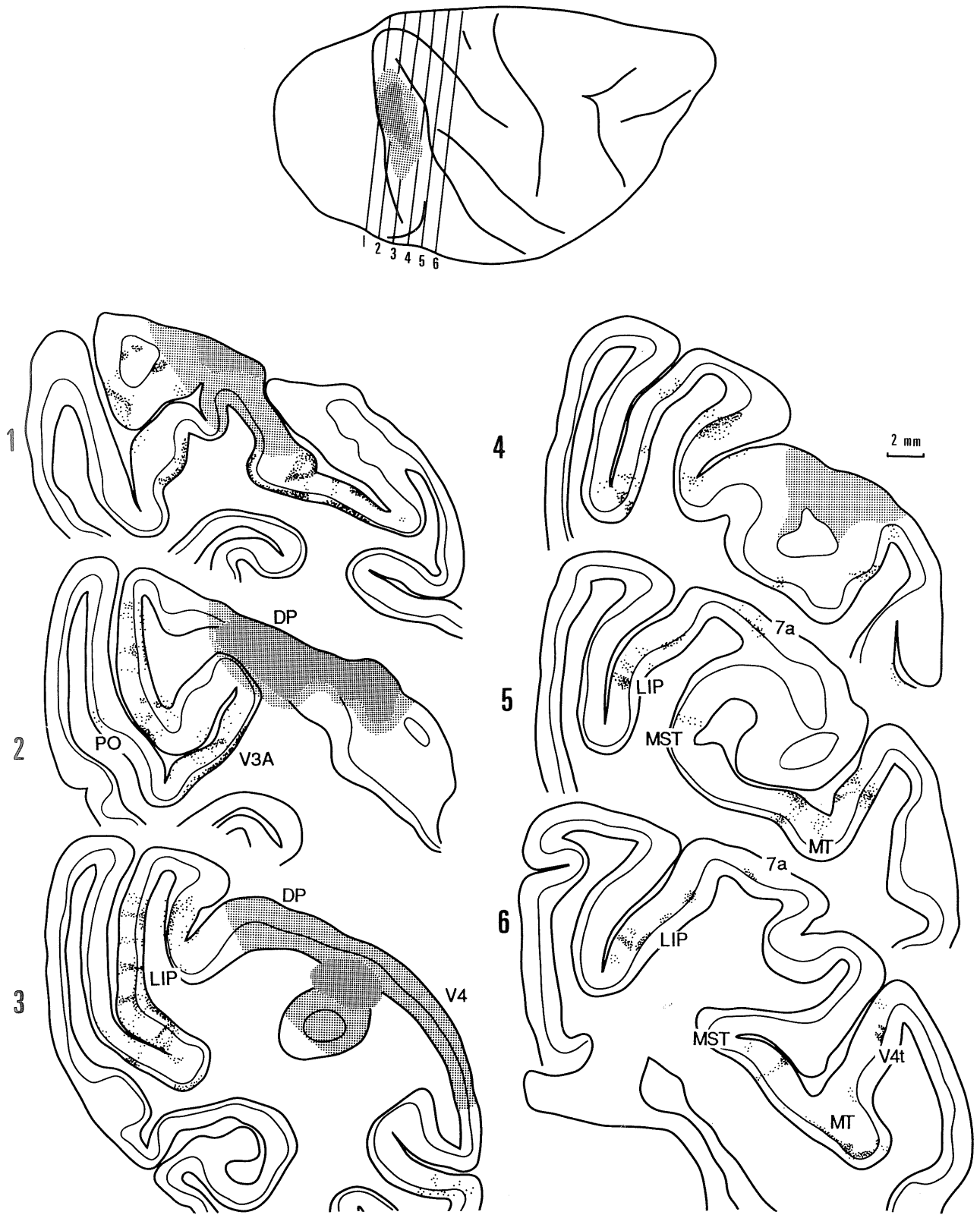
Fig. 12. Seven .5 μl injections of TAA were made in area DP, with spread of tracer into the dorsal aspect of area V4, of the right hemisphere of case 9. The shading in the upper inset and on the cross sections shows the extent of the injection site on the surface of the hemisphere. The heavier and lighter stippling corresponds to heavier and lighter labelling over both cell bodies and neuropil. The same relative shading of the injection site is used in Figures 12, 14–17.

Fig. 13. Flattened reconstruction of case 9, also illustrated in Figure 11. Multiple injections of TAA were made primarily into area DP, with some spread into V4, in the right hemisphere. The extent of the injection site is indicated by the continuous labelling. Terminal labelling is indicated by the strips of labelling that are confined to the contour lines marking the individual serial sections.

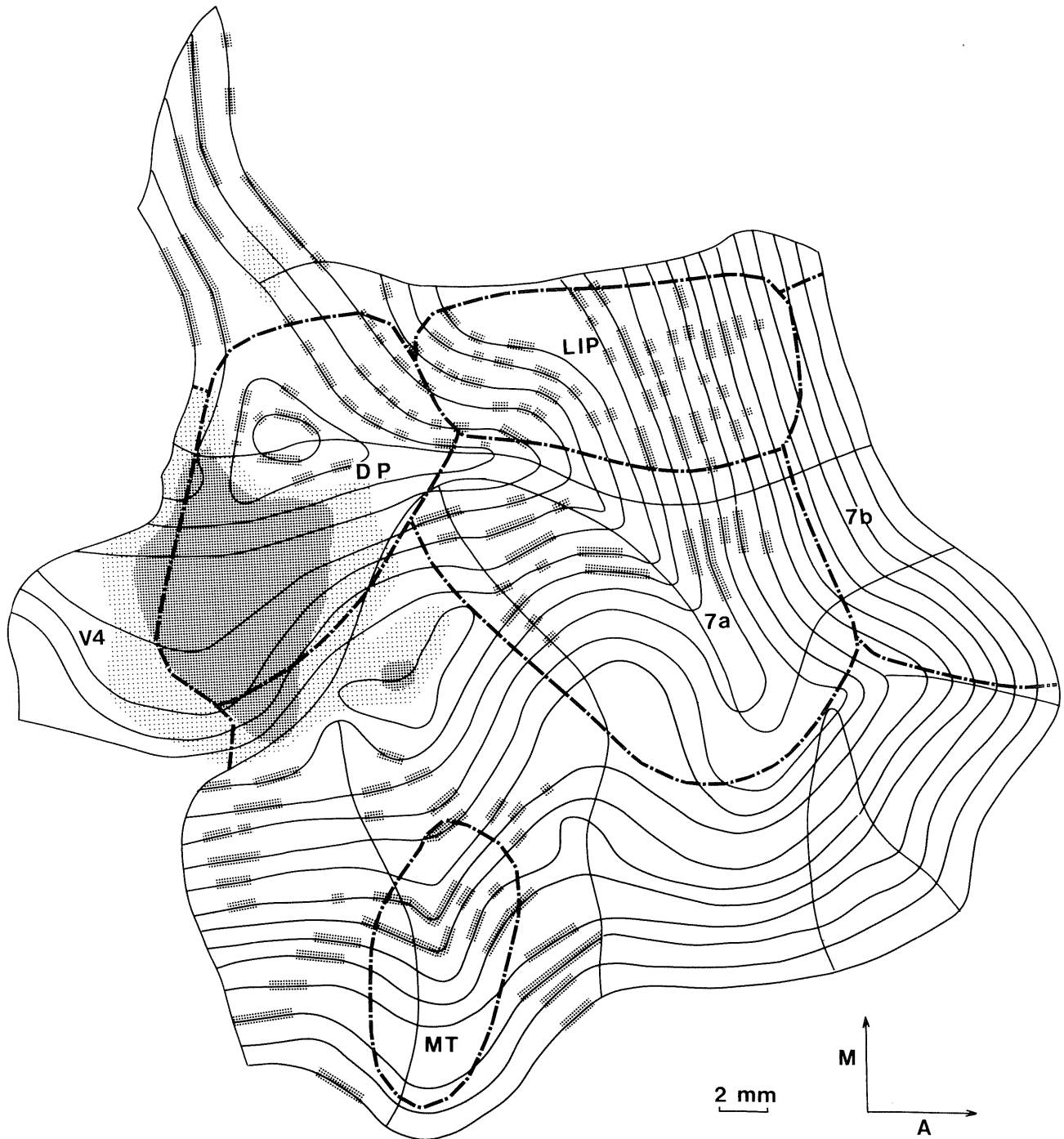increase in activity for eye position in a particular direction. For instance, progressively downward fixations for the cell in Figure 22 produced increments in tonic activity. To examine this observation more quantitatively, a two-dimensional linear regression analysis was performed to see if a plane could be used to model the change in cell activity with changes in horizontal and vertical eye position (Klein-

baum and Kupper, '78; Netter and Wasserman, '83). For instance, would a plane tilted up for downward fixations best fit the data shown in the left panel of Figure 22.

Of 65 eye position cells analysed in this fashion only one was found to have no statistically significant change in activity with eye position. Nineteen of the cells had planar gain fields (model $P < .05$) with no significant lack-of-fit
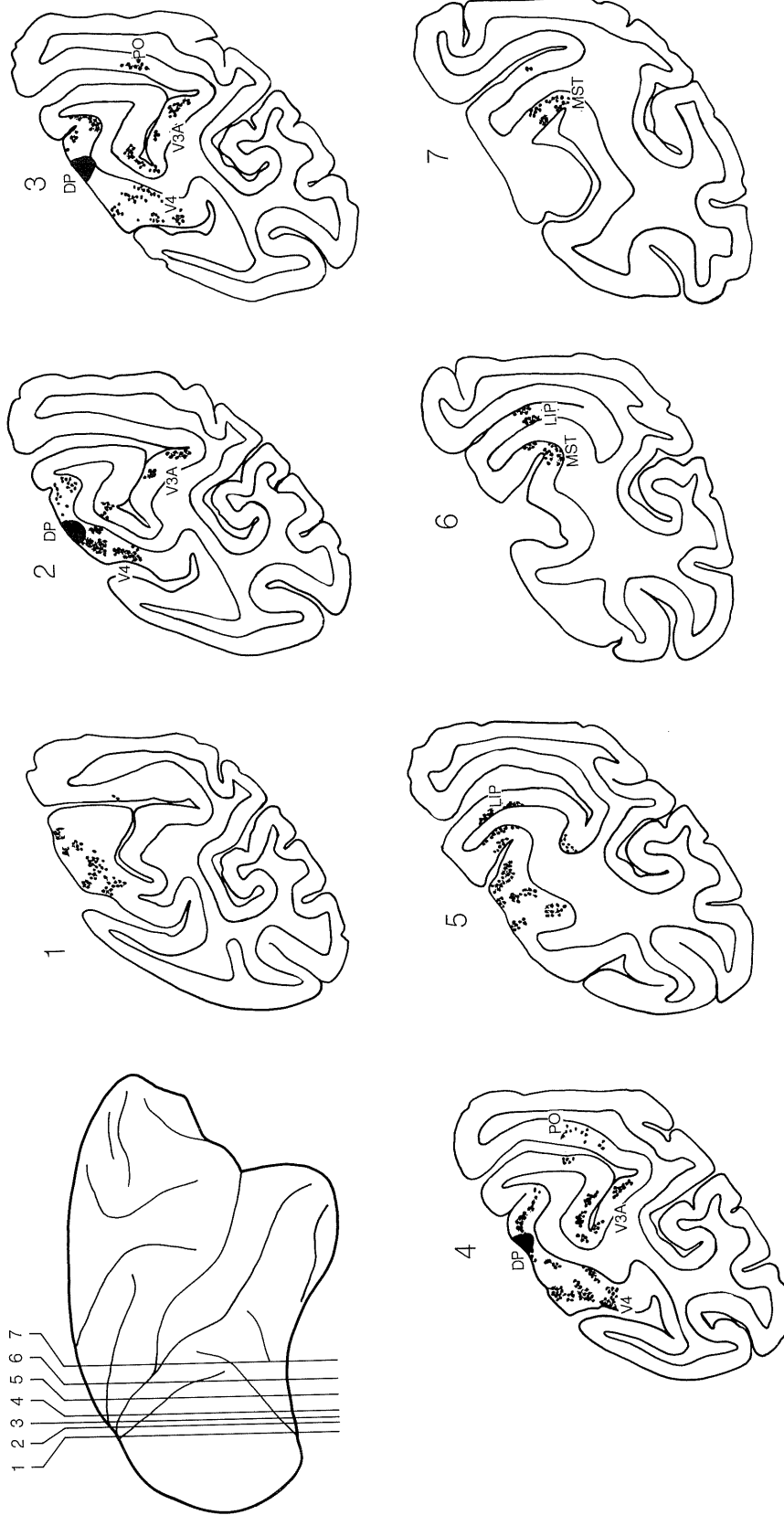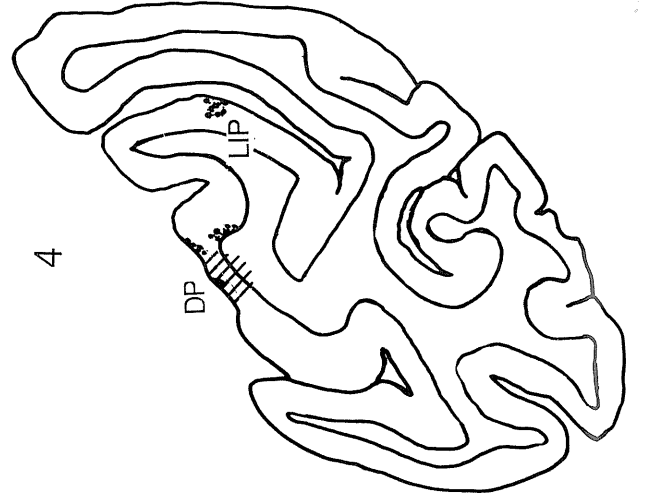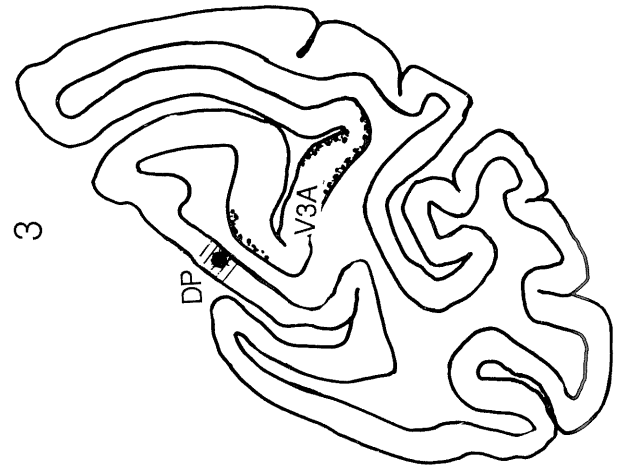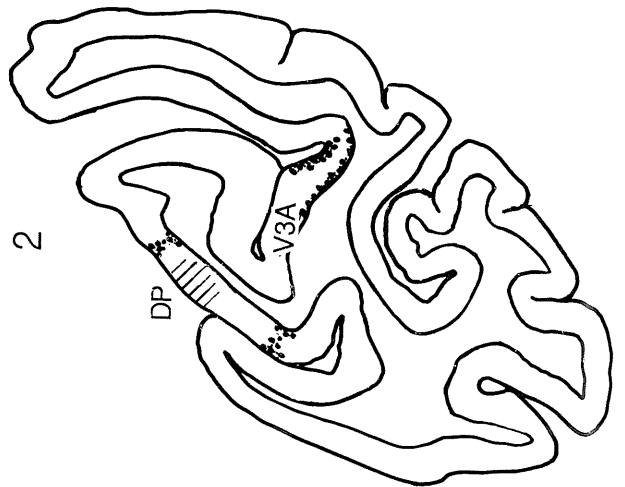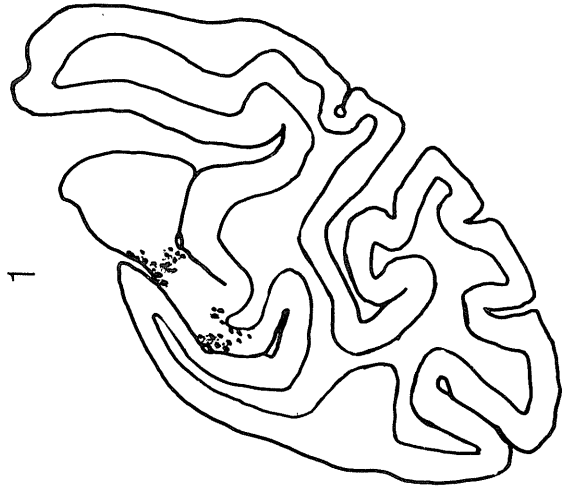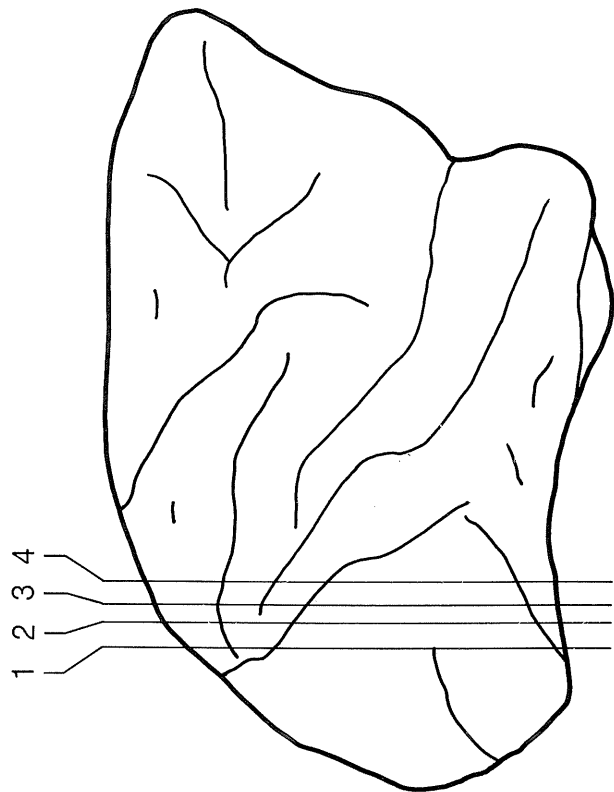
(lack-of-fit $P > .05$). In these cases a plane is the best fit to the data. For forty-two of the cells there was a significant planar component (model $P < .05$) but also a significant lack-of-fit ($P < .05$), indicating that a plane is not the best fit to the data. Usually the gaze fields of these cells appear largely planar but with bumps or depressions that deviate from a perfect plane. The data illustrated in the left panel of Figure 20 is an example of one of these gaze fields. Finally, only three cells had gaze fields that had no planar component (model $P > .05$) but were nonetheless modulated by eye position (lack-of-fit $P < .05$). These gaze fields were peaks rather than planes. This analysis showed that 94% of the gaze fields were planar or had significant planar components. The r^2 values ranged from .089 to .882 with a mean of .402.

Thirty-one of the cells with significant planar components were recorded from area 7a and 30 from area LIP. The gaze fields of these cells were further analysed to determine if there was any difference between gaze fields for cells in these two areas. In Figure 23 A and B are the separate horizontal and vertical slopes for the planar components of the gaze fields. Only slopes that were significant are plotted; for instance, a gaze field fit by a plane tilted downward will have a significant vertical slope but no significant horizontal slope. It should be noted that the slope represents the change in background firing rate (in the absence of visual stimulation) per degree of eye position. The intercept represents the background firing rate (in the absence of visual stimulation) when the animal fixates straight ahead (i.e., at coordinates 0,0).

As can be seen, there is little difference for the slopes (Fig. 23C), between gaze fields recorded from area 7a and area LIP neurons. However, the intercepts were larger for area LIP compared to area 7a. Figure 23D shows the linear fits for significant, positive horizontal slopes for both area 7a and LIP neurons. Again notice that these slopes look very similar for the two cortical fields.

In a second analysis we compared the directions of the gradients of the planar fits for the two areas. The gradients are the directions of greatest positive slope of the planes. For instance, a cell which increases activity equally for looking up or into the contralateral visual field would have a gradient direction of 45°, whereas one that has equally increasing activity for downward and ipsilateral gaze would have a gradient direction of 225°. The gradients are determined by computing the tangents of the ratio formed by the vertical and horizontal slopes. Figure 24A shows the distribution of gradient directions for the area 7a population and Figure 24B shows the directions for the area LIP population. Figure 24C shows the distribution of directions for contralateral and ipsilateral deviations. There is no statistical difference between contralateral and ipsilateral directions for either area 7a or LIP (χ^2 goodness-of-fit test) and the ipsi-contra ratios between the two regions is also not statistically significant (χ^2 test of association). On the other hand Figure 24D indicates that both area 7a ($P < .001$) and area LIP ($P < .05$) have a significantly larger number of gradient directions pointed downward and the up/down ratio is not significantly different between the fields. Finally the bar graph in Figure 24E indicates that area 7a ($P < .01$) and area LIP ($P < .10$) have significant and nearly signifi-

cant preferences for directions along the cardinal axes compared to the diagonal axes. Again, no significant difference was found for the Cardinal/Diagonal ratios between the areas.

Eye position signals were also found for area DP neurons. We mapped gaze fields for five area DP cells and found them to be quite similar to the gaze fields recorded for areas 7a and LIP.

The above data indicate that the gaze fields of area 7a, LIP, and DP cells are very similar in their distributions of slopes and gradient directions. The only difference between the areas was the larger intercept values for area LIP.

Light sensitivity. Complete mappings of visual receptive fields under computer control were made for 95 neurons. Sixty-four of these cells were from area 7a, 14 from area LIP, and 17 from area DP. The receptive fields were mapped by flashing 1° or 6° diameter stimuli at 17 locations in the visual field. The stimulus locations consisted of the fixation point and four equally spaced locations on four concentric circles spaced 10° apart out to a 40° radius (Fig. 26B). The flashes were 500 msec in duration and the animals were trained to ignore the stimulus and attend to the fixation point in a dimming detection task.

Figure 25 shows representative examples of area 7a receptive fields. Each sector is shaded proportional to the average activity evoked by the stimulus flashed in the center of that sector. The overall maximum diameter of the shaded areas is 100° of visual angle with the center representing the fixation point. As can be seen, area 7a receptive fields are usually large and bilateral. Typically there is a single peak of maximum activity with a smooth fall-off in activity in all directions similar to the cell illustrated in the upper left-hand panel. However, it is not uncommon to find cells with more than one peak of activity as is illustrated by the receptive field in the upper right-hand panel. The receptive fields can be centered on the fovea (middle left panel) or peripheral locations (middle right panel). There can be holes in the receptive fields as well. Sometimes these holes are located at the fovea (lower left panel), a pattern first described by Motter and Mountcastle ('81) which they termed "foveal sparing." However, the holes can also be located at peripheral field locations, as indicated by the panel on the lower right.

To quantify further the receptive field properties of area 7a neurons, the radius from the highest peak of activity to the average fall-off to 37% of the peak activity was measured for 61 cells. The distribution of radii is plotted in Figure 26A. The mean radius was 22.0° for an average diameter of 44.0°. In Figure 26B are plotted the locations of the centers of the largest peaks of the receptive fields. Each dark circle is positioned at one of the 17 visual field locations that were tested with the flashed stimuli and the diameter of the circle is proportional to the number of cells with peaks at that location. It can be seen that the centers of the receptive fields tended to be located in the contralateral visual field and there may also be a bias for the lower visual field. However, since the average 1/e diameters of the receptive fields is 44°, a large number of the receptive fields are bilateral. Moreover, 27 of the receptive fields had their centers located around the vertical meridian, and all of these cells had bilateral receptive fields. Many of the receptive fields include the fovea, although most of the peaks occur at 10° or 20° peripheral to the foveal region.

No retinotopic organization was found for the receptive fields in area 7a. Figure 27 shows the receptive fields of 32

Fig. 15. Labelling from a single .05 μl injection of TAA made into area DP in the right hemisphere of case 14.
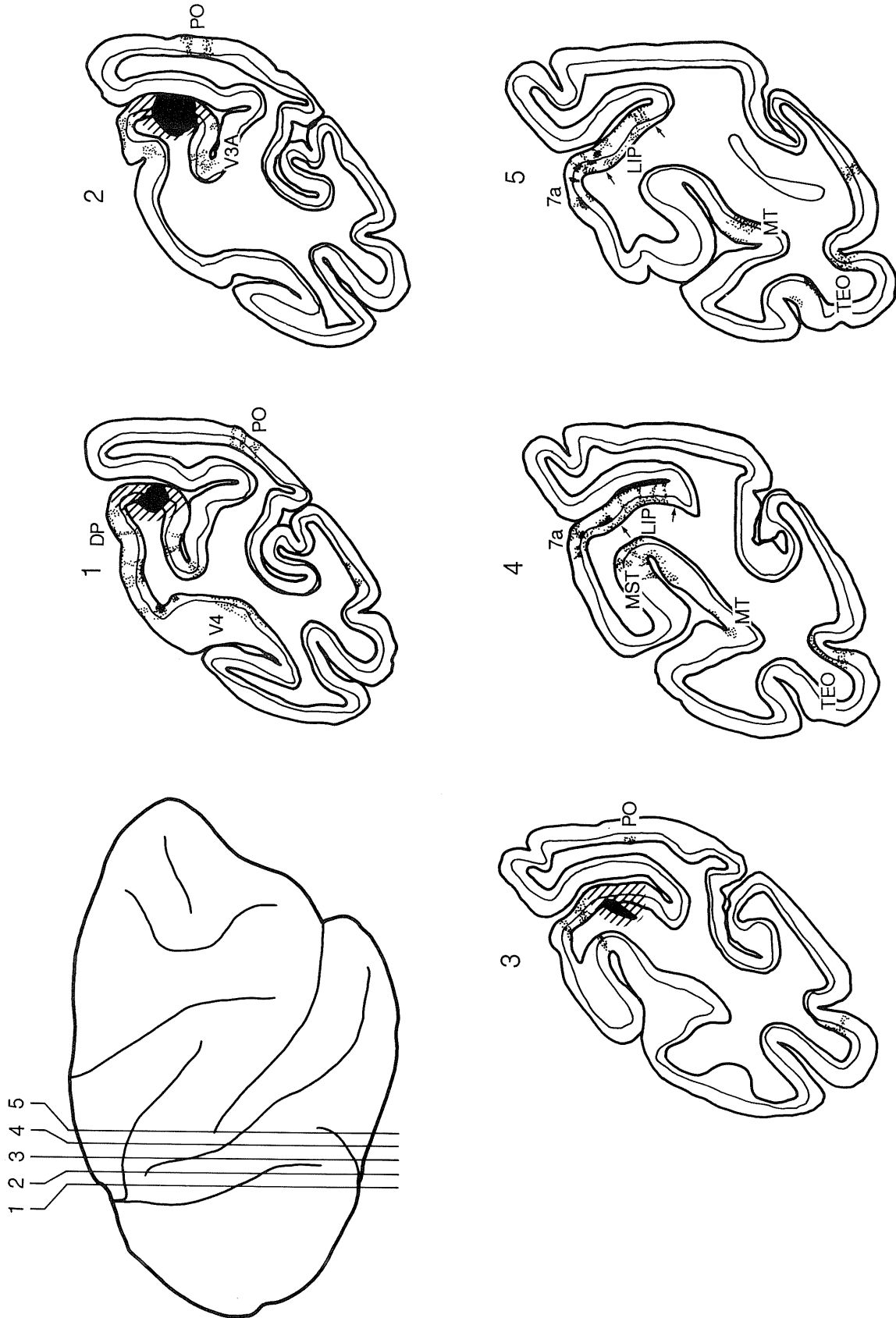
Fig. 16. Labelling from a single .4 µl injection of TAA made into area LIP in the left hemisphere of case 6.
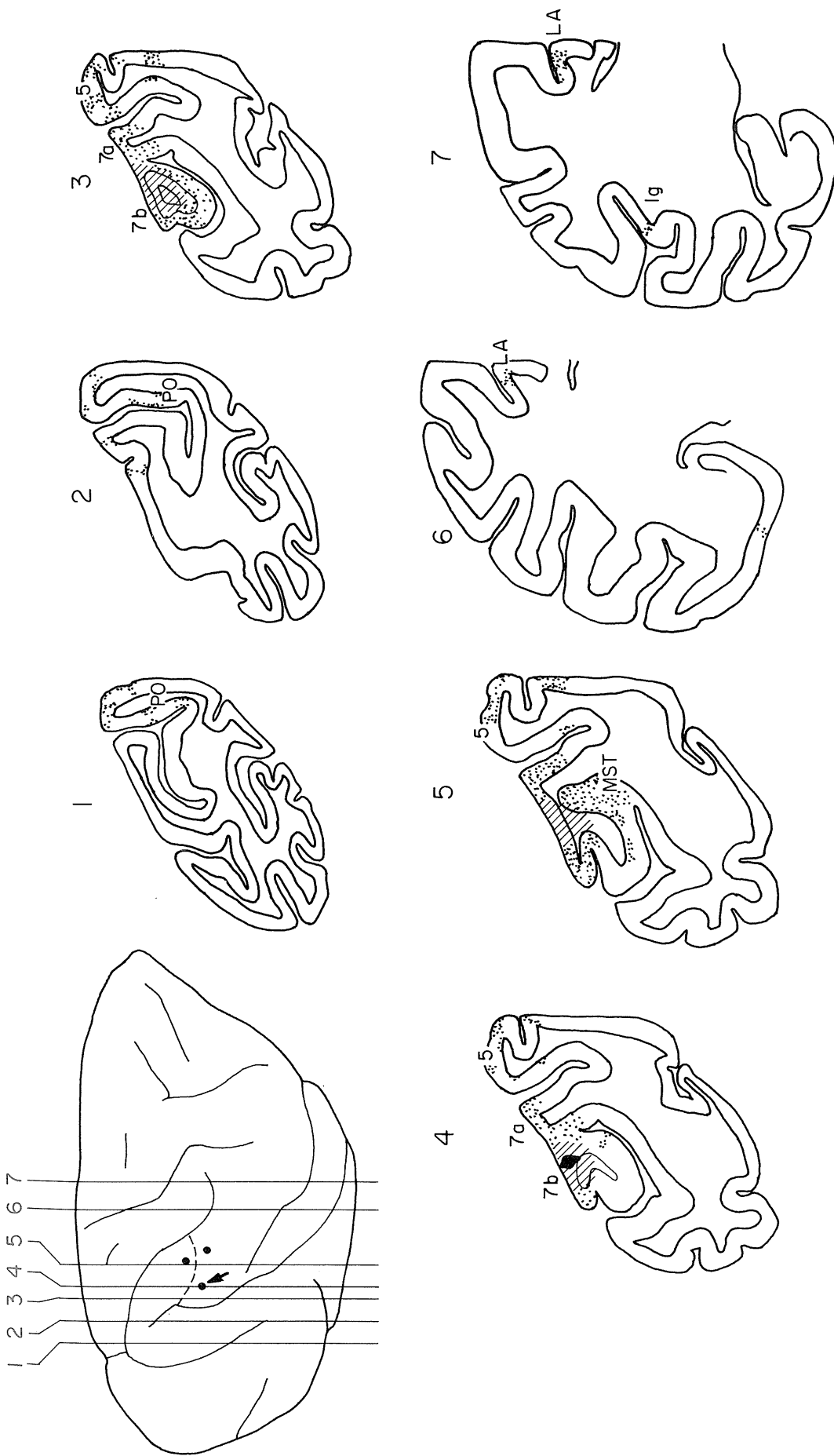
Fig. 17. Labelling from a single .5 μl injection of TAA made into area 7b in the left hemisphere of case 10. The arrow in the **inset** shows the location of the injection on the surface of the hemisphere. The dotted line indicates the 7a, 7b border and the two dots without arrows the sites of injection of NY into area 7a and FB into area 7b. Labelling from these two retrograde injection cases is shown in Figures 7 and 10.
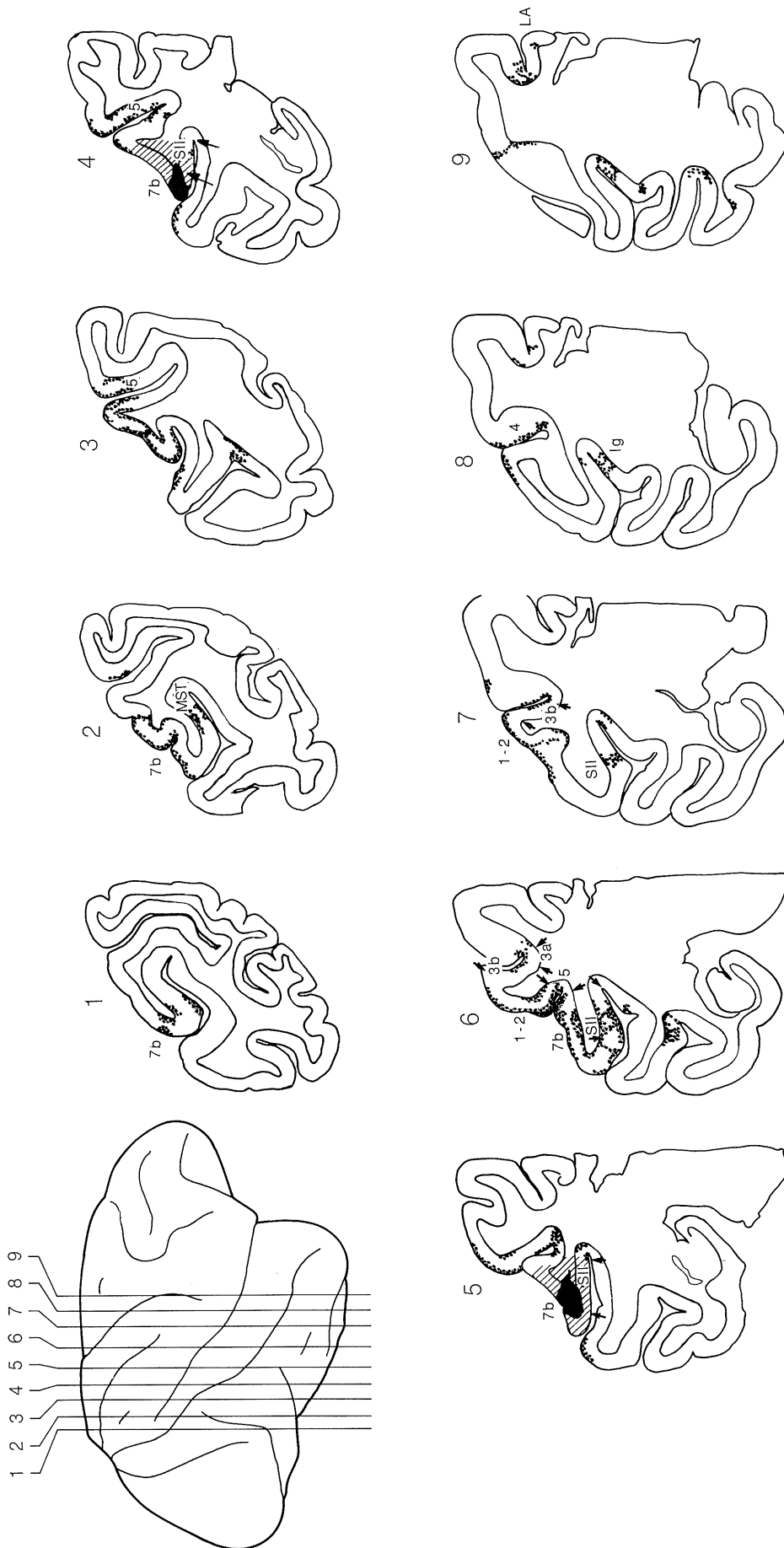
Fig. 18. Label from a single .4 μl injection of TAA made into area 7b in the left hemisphere of case 7. Tracer also diffused into area SII.
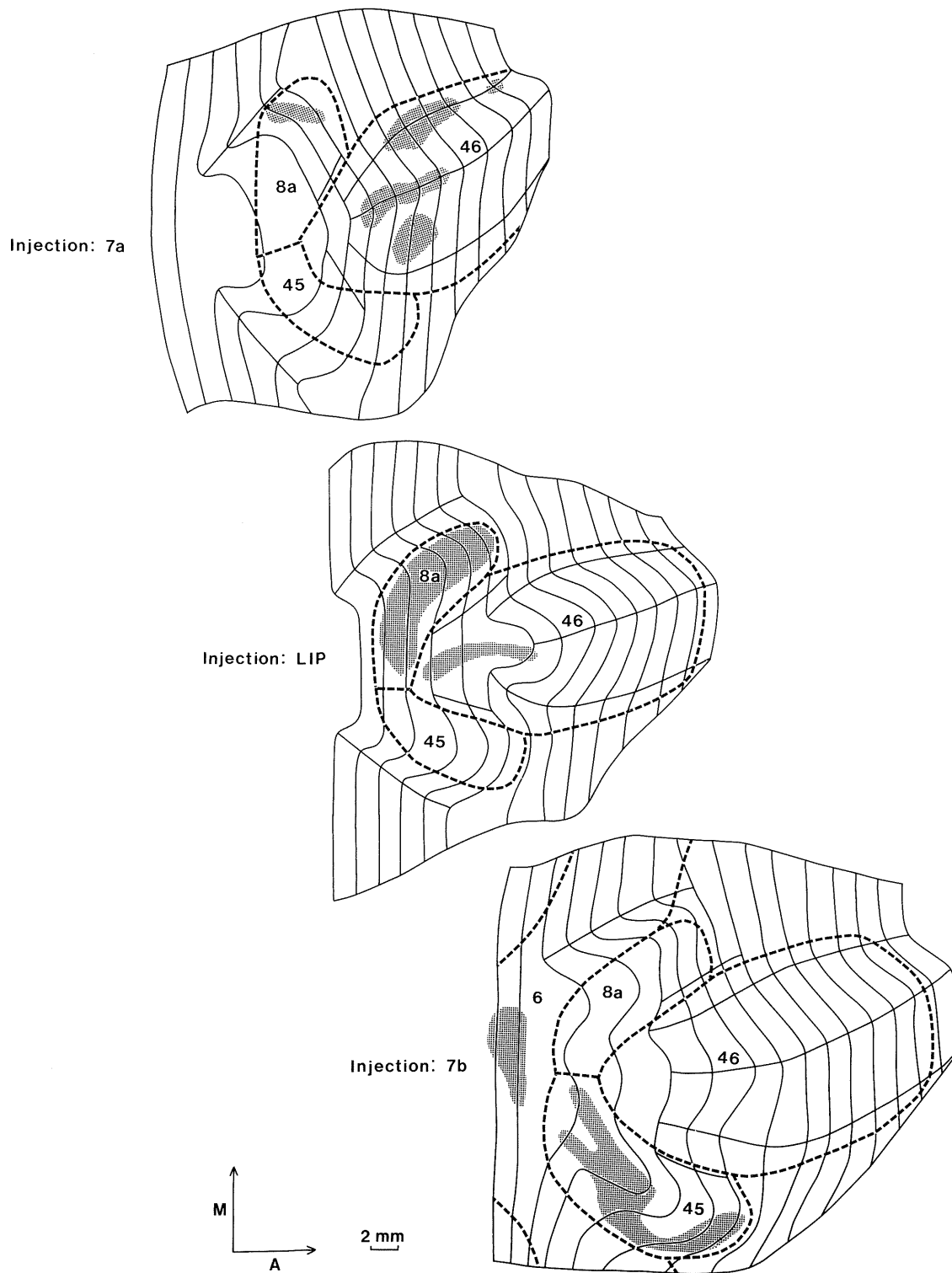
Fig. 19. Flattened reconstructions of the left frontal lobes of three monkeys showing the patterns of labelling after injections of TAA into different cortical areas in the ipsilateral posterior parietal cortex. In the **top illustration** labelling resulted from a .5 μl injection into area 7a. The pattern of labelling in the **middle illustration** resulted from a .4 μl injection into area LIP, and, for the **bottom illustration,** from a .4 μl injection into area 7b. The cortical areas were determined in each case by using the cytoarchitectonic criteria of Walker ('40).

ST

IP

Figure 20

A. Visual, Somatosensory

B. Saccade Related, Eye Position

• VISUAL

+ SOMATOSENSORY

▲ SACCADE
   RELATED

□ EYE POSITION

|——————|
   5mm

Fig. 21. Flattened reconstructions of one hemisphere showing the locations of cells A) with visual and somatosensory responses and B) with eye position and saccade responses. Saccade responses were for saccades to visible targets in either a lighted or darkened test chamber.

area 7a cells and 4 area DP cells mapped from one hemisphere. The dark areas represent regions of greatest activity within the receptive field. The outer circles of the largest receptive fields are 100° in diameter and represent the maximum extent of the receptive field that was tested. As can be seen, no clear retinotopic organization is discernible.

Area 7a cells were more likely to have the receptive field peak in the ipsilateral visual field. Ten of 64 area 7a receptive field peaks were ipsilateral, whereas only 1 of 13 LIP peaks and only 1 of 17 area DP peaks were in the ipsilateral field. Area 7a fields were the largest, followed by area DP, followed by area LIP. Area DP receptive field peaks were concentrated in the lower visual field with 10 peaks in the lower field, 6 along the horizontal meridian, and only one in the upper visual field.

Saccade activity. The saccade activities of a large portion of the cells used in this study were also reported in Andersen et al. ('87) and Andersen and Gnadt ('89). In those studies it was shown that the saccade responses of IPL neurons were not an artifact of visual stimulation by using the special controls that separate saccade from visually evoked activity. At the time, the borders of areas LIP, 7a, and DP were not as well understood as in the present study,

Fig. 20. A Nissl stained coronal section through the right posterior parietal cortex of case 15. The hollow arrow shows the location of the needle track from a .05 μl injection of NY made into area 7a. The functional organization of this hemisphere was mapped prior to the tracer injection by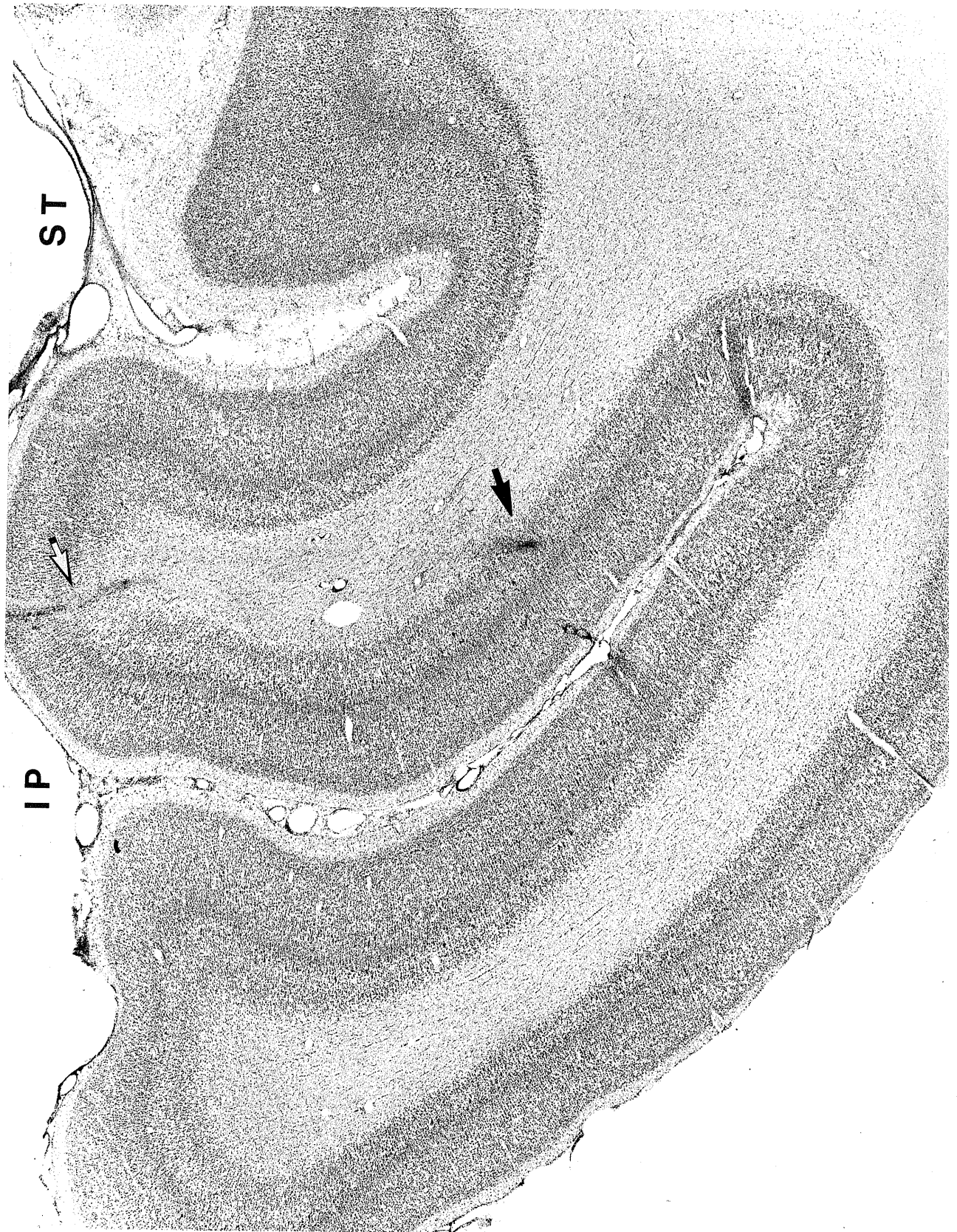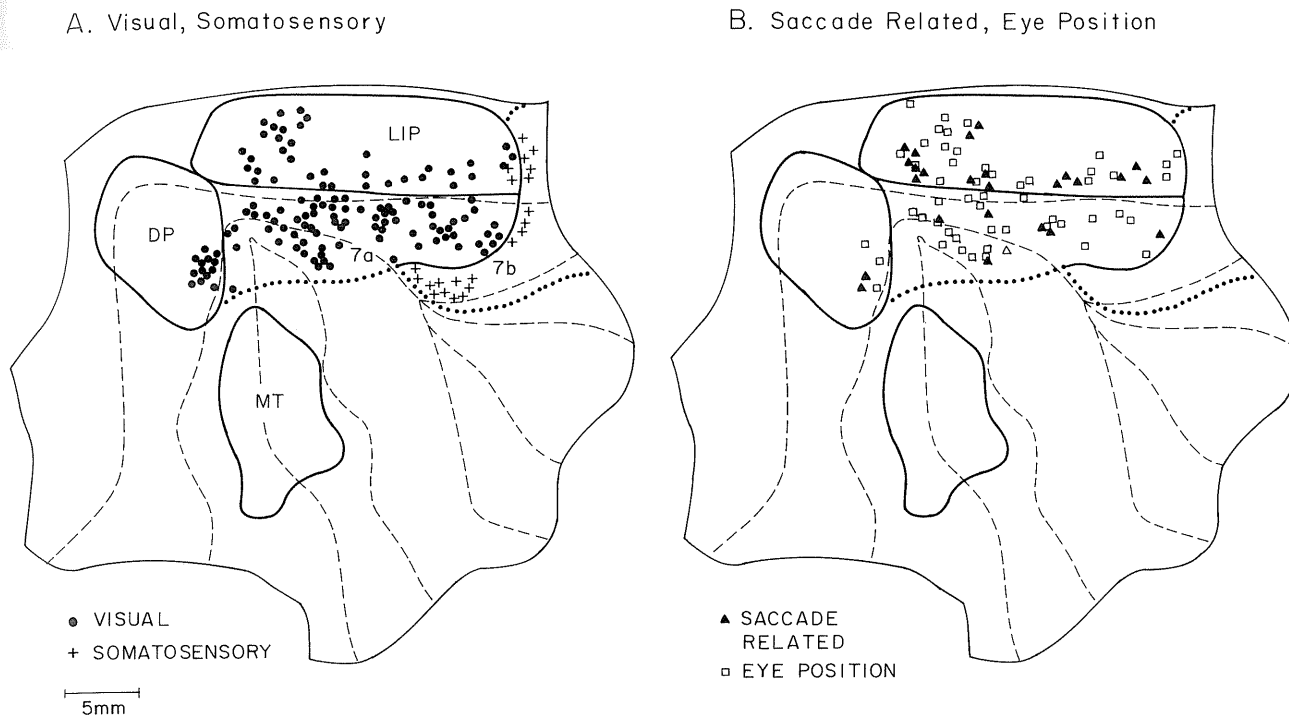 using single cell recording techniques in the behaving monkey. The solid arrow indicates an electrically induced lesion made in area LIP at the end of one of the recording tracks in the functional mapping experiments.

so we have reevaluated this data with special emphasis on the regional variations of saccade properties.

One hundred ninety cells were first tested in a task in which the animal makes a saccade to a visual target in either a lighted or darkened test chamber. In this task the fixation light goes off, and the target appears simultaneously and the animal is required to make a saccade to fixate the new target. This task does not separate saccade activity from visual stimulation that can potentially arise from the target stimulus, the offset of the fixation point, or, in the lighted chamber, the sweeping of the image of the visual background across the retina during the eye movement. One hundred three area 7a neurons were tested and 60 (58%) were found to be active in this task. Twenty-four of 42 area LIP cells (57%) and 35 of 45 area DP cells (78%) were also found to be active in this task. Of the 60 neurons from area 7a that were active in the above task, 45 were further tested in the special saccade tasks developed to separate visual from saccade related activity. Twenty-two of these area 7a cells (49%) were determined to have true saccade-related activity. Six of ten area LIP cells tested in this manner were found to have true saccade activity and, similarly, 14 of 22 area DP cells were also found to have saccade activity. Of the 42 cells with true saccade-related responses, only 5 had presaccadic activity; interestingly all 5 presaccadic cells were from area LIP. The area LIP responses were among the largest in terms of evoked firing rate. The mean latency was 96 msec postsaccadic for area 7a, 80 msec presaccadic for LIP, and 198 msec postsaccadic for DP. Of the cells with true saccade-related activity, 80% also responded to visual stimuli. Thus, like the eye position cells, these neurons generally received a convergence of visual and oculomotor-related signals. The direction tuning of the saccades usually

VISUAL RECEPTIVE FIELD
fixation at (0°,0°)

10°

GAZE FIELD
9 fixations at +'s

10°

Fig. 22. An example of an area 7a neuron that has both a fixation component and a visual component of activity. **Left panel**: The animal fixates a point of light in the otherwise total darkness at 9 locations on the screen. The post-stimulus-time histograms show that the cell is most active when the monkey fixates down. **Right panel**: The animal fixates only the center position on the screen and the receptive field is mapped with the visual stimulus at 9 locations. The receptive field is large, as is typical for cells in area 7a, with responses at the fovea and at least 20° to the right and 20° down. Histogram scales: Horizontal, 1 sec/div; vertical, 6 spikes/sec/div.

A) Horizontal Slope

B) Vertical Slope

C) Intercepts

D) Horizontal Linear Fits
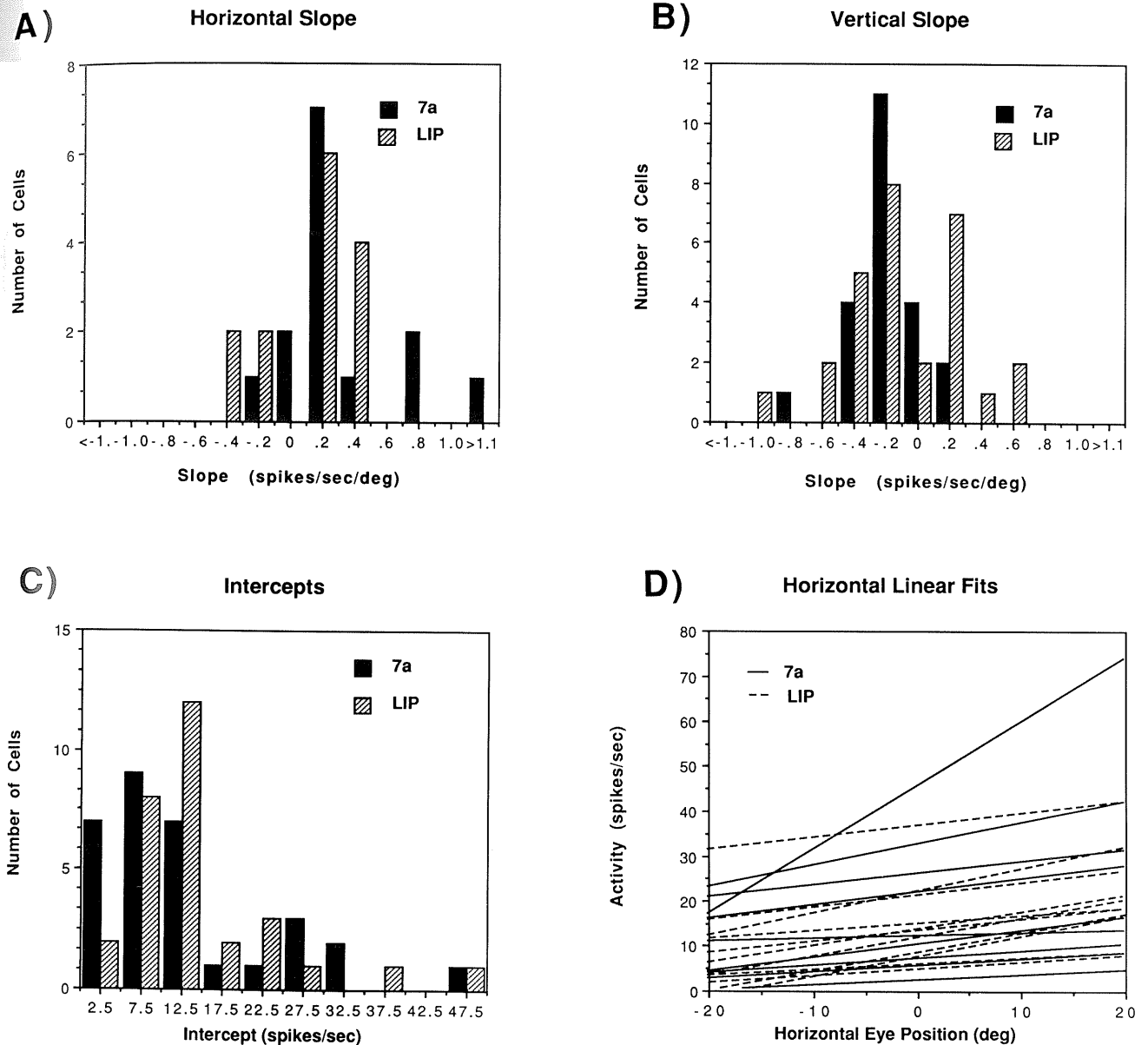
Fig. 23. **A:** Distribution of horizontal slopes of gaze fields for area 7a and LIP neurons. Only significant slopes are plotted. **B:** Distribution of vertical slopes. **C:** Distribution of intercepts of gaze fields for area 7a and LIP neurons. **D:** Linear fits for cells with significant positive horizontal slopes.

matched the direction from the fovea of the peak of the visual receptive field. There was no apparent segregation of saccade and eye-position signals in areas 7a or LIP. Cells with eye-position responses were intermingled with cells showing visual responses, and four of the cells with true saccade responses also had significant gaze fields.

The above data indicate that the inferior parietal lobule can be divided into a caudal region that includes areas 7a, LIP, and DP and is visual and visual-motor in function, and a more rostral region that encompasses area 7b and is more involved in somatosensory and somatomotor functions. Area 7a and LIP differ in terms of visual receptive fields; they are larger and bilateral for area 7a neurons and smaller and contralateral for area LIP neurons. Area DP also

contains visually sensitive cells with large receptive fields with centers typically in the lower contralateral visual field. Eye-position activity was found in areas 7a, LIP, and DP (Fig. 21B). Quantitative analyses indicated that the eye-position properties of area LIP and 7a neurons are quite similar. Areas 7a, DP, and LIP also have cells with saccade-related activity (Fig. 21B). The saccade responses of area LIP neurons are brisk and are more likely to be presaccadic than those of areas 7a and DP.

DISCUSSION

In the experiments reported here, several possible sources of cortical visual input to areas in the inferior parietal lobule

A) 7a Gradient Directions

B) LIP Gradient Directions

C) Contra-Ipsi

D) Upper-Lower

E) Cardinal and Diagonal Gradients
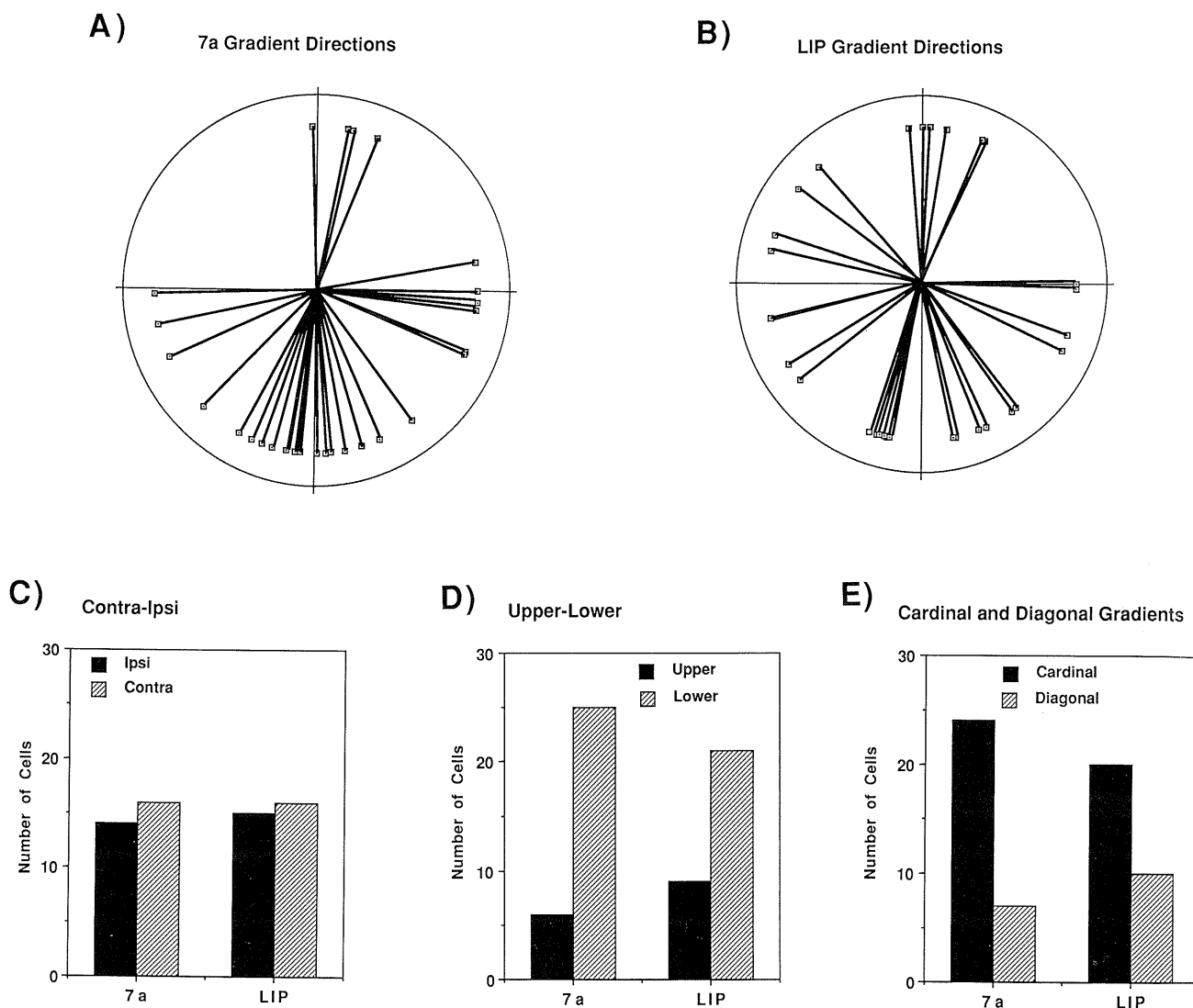
Fig. 24. **A:** Gradient directions for 31 area 7a neurons with gaze fields. Contralateral gaze is to the right. **B:** Gradient directions for 30 area LIP neurons with gaze fields. **C:** Comparison of the numbers of contralateral and ipsilateral directed gradients for area 7a and LIP gaze fields. **D:** Comparison of the numbers of upward and downward directed gradients for area 7a and LIP gaze fields. **E:** Comparison of the numbers of gaze fields with directions in the cardinal or diagonal directions. To be classified as having a cardinal direction a gradient direction must fall within a 45° window centered on any of the four cardinal axes. Likewise, diagonal directions must be within a 45° window centered on any of the four diagonal directions.

have been identified. In the course of these experiments the connections of two new areas, DP and LIP, have been mapped, and several previously unobserved connections of areas 7a and 7b have been described. The laminar patterns of connections of these various areas have been investigated in order to establish a hierarchy of visual information processing. Finally, the functional and anatomical organization of the inferior parietal lobule has been further elaborated by these experiments. Table 2 summarizes the major distinguishing functional and anatomical features for areas 7a, 7b, LIP, and DP.

Hierarchy of cortical connections

Figures 28 and 29 show hierarchies of connections that can be constructed by making certain assumptions about the patterns of laminar labelling. It must be emphasized

that this hierarchy is hypothetical and is inferred from the laminar patterns of connections found in earlier parts of the visual pathway where the direction of information processing is somewhat better understood. Only after more is known about the mechanisms of visual information processing in these higher cortical areas will it be possible to determine if this hierarchy is correct. However, we believe that the formulation of such a processing structure will serve as a useful model for physiological experimentation. By having some idea of the direction of information flow, we will find it easier to sort out how more elementary processing in the earlier parts of the pathway are combined to produce more elaborate processing at higher levels in the pathway.

It must also be emphasized that the laminar pattern of terminal labelling is often not stereotypical and easily categorized into the feedforward, feedback, and mixed and

TABLE 2. Major Distinguishing Features[1]

	7a	7b	LIP	DP
Physiological	Visual with large, bilateral receptive fields, eye position, some saccade-related (mostly postsaccadic) cells	Somatosensory	Visual, with contralateral receptive fields, many saccade-related (half presaccadic) cells, eye position	Visual, eye position
Connectional				
Frontal lobe	Areal 46*, 8a, 11, SEF, 45	Area 45, 6, 12	Area 8a*, 46	Weak to 46, 8a
Extrastriate visual areas	PO, DP, LIP, MST, FST, STP, IT	MST, PO, STP, IT	PO, DP, 7a, MST, MT, V4, V3A, V3d, V3v, TEO	V3A, LIP, 7a, V4, PO, MST
Somatosensory	None	Area 5, insular cortex (Ig)	None	None
Other temporal lobe	TFl, TFm, presubiculum	None	TF	None
Other parietal lobe	PGm, MIP, PIP, MDP	PGm	None	None
Cingulate	LC*, LA	LA*, LC	None	None
Pulvinar	Medial	Oral	Lateral	Lateral
Superior colliculus, pretectum	DPN	None	SC, APN	SC

[1]Asterisk = predominantly.

intermediate classes. For example, the projection from area LIP to TF is strong to both layers IV and VI. The high variability in laminar labelling patterns between areas is probably not due to technical considerations, since these different patterns existed within single experiments and between areas of approximately the same transport distances. Thus they probably do not reflect differences in the ratios of terminal versus fiber labelling but rather real differences in the distribution of terminals. The unique nature of laminar labelling often required us to make judgements about which patterns are feedforward and feedback. Generally, if the highest densities of terminal label were in the middle layers, then this constituted a feedforward categorization, and if the highest densities were in the superficial and deep layers, a feedback categorization.

Source of visual inputs to area 7a

When the experiments reported in this paper were begun an important question involved determining the source of visual inputs to area 7a. As can be seen in Figure 28, there are many possible pathways for visual information to flow into area 7a. Direct paths exist in the projections of several visual extrastriate cortical areas into area 7a, including areas PO, MST, DP, and STP. Area V4, which is believed to have an important role in pattern and color processing, can provide inputs to area 7a through area DP. There are two potential visual motion processing pathways into area 7a from area MT via either area MST or area LIP. Interestingly, Ungerleider and Desimone ('86a) have shown that there is a direct projection from area VI to a small area medial to the heavily myelinated portion of area MT that they called MTp that includes part of the densely myelinated zone (DMZ). Cortical areas in this general region, including a portion of the DMZ, project to area 7a. Thus, it is possible that there may be a two-step route of visual information flow from area VI to MTp and from MTp to area 7a. Double labelling experiments in single animals will be required to demonstrate conclusively that such a direct link exists.

Figure 28 shows that the visual areas in the occipital and temporal areas of cortex are so densely interconnected with the various areas in the inferior parietal lobule, and the visual areas in the inferior parietal lobule with each other, that there is an enormous number of possible pathways for visual information to flow. Perhaps, instead of trying to list all the possible pathways of visual information flow from area VI to the posterior parietal cortex, a more useful view is that there exists a densely interconnected network of connections within these regions and that each cortical area,

including area 7a, is one node in this highly distributed network. An important goal is to determine what different computations are being performed at each node in this network. An even more challenging question is how the sum of the various parts of this complex network leads to mental functions and behavior. To these ends, a model of a hierarchical structure within this network should be helpful in elucidating its functions.

In Figure 29 the extrastriate visual pathways have been removed, and the connections of the areas 7a, 7b, DP, and LIP with other cortical areas are shown. Again there appears to be a hierarchy based on laminar labelling patterns. Of particular interest is the observation that several of the high level cortical areas, including the cingulate cortex, insular cortex, areas in the inferior parietal lobule (7a, 7b, and PGm), and the parahippocampal gyrus appear to be at approximately the same level in the hierarchy. These areas and the prefrontal cortex are all massively, reciprocally interconnected with one another. Interestingly, the medial pulvinar is part of this same network having reciprocal connections with all of these regions. The elegantly modular organization of these connections within the medial pulvinar for the prefrontal and inferior parietal lobules was studied by Asanuma et al. ('85); and it has been proposed by Andersen ('87) that this modular, partially overlapping structure may represent the anatomical substrate of a mechanism for coordinating activity and transmission within this network. This regulation may include functions commonly labelled as selective attention. Figure 29 indicates that, even at the high level that includes the inferior parietal lobule, cingulate gyrus, insular cortex, prefrontal cortex, and inferotemporal cortex, the brain is still organized along the same two general plans that are evident in the early stages of processing in the extrastriate cortex (illustrated in Fig. 28). The first of these rules holds that brain functions are processed in a distributed fashion in complex and highly interconnected networks, an idea that has been proposed and discussed by several investigators (Mountcastle, '78; Mesulam, '81; Andersen et al., '85a; Asanuma et al., '85; Andersen, '87; Goldman-Rakic, '88). The second suggests that there is a great deal of structure in these networks, and, in particular, there appears to be a hierarchy of feedforward and feedback pathways.

Functional organization of the inferior parietal lobule

The first reports of single cell recordings in the inferior parietal lobule of behaving monkeys were made in the early '70s by Mountcastle and co-workers (Lynch et al., '73a,b,
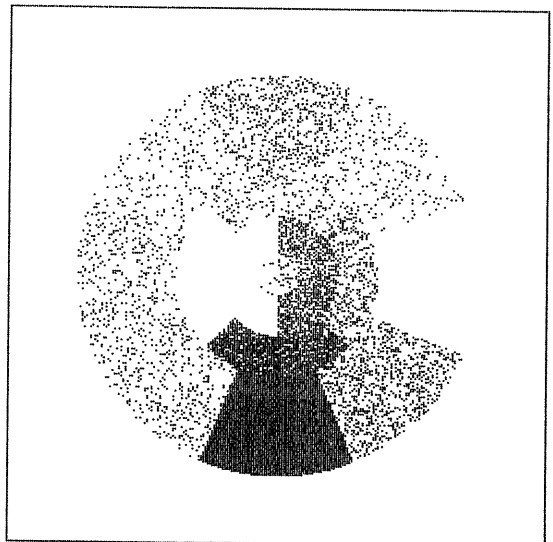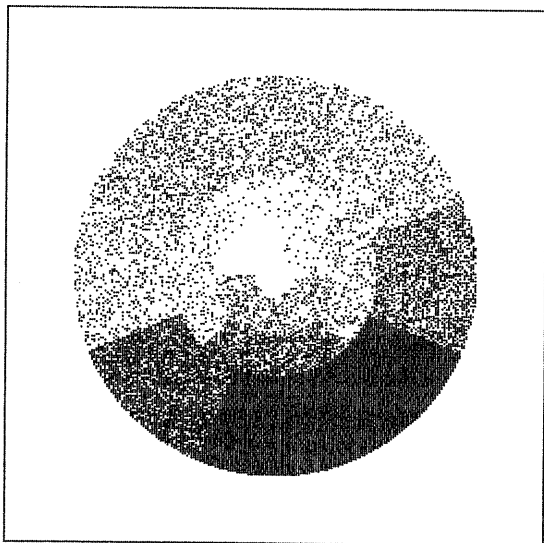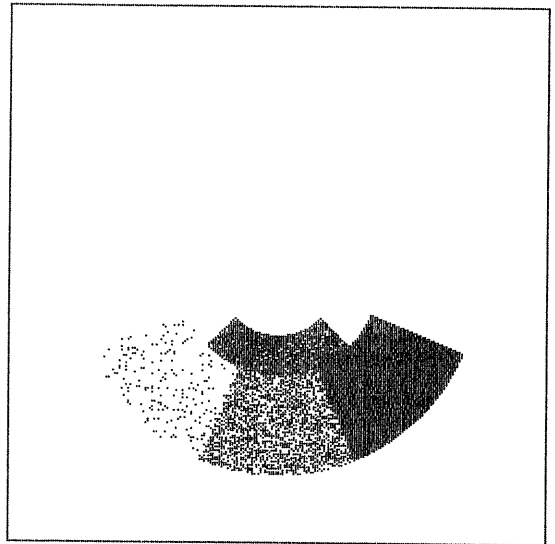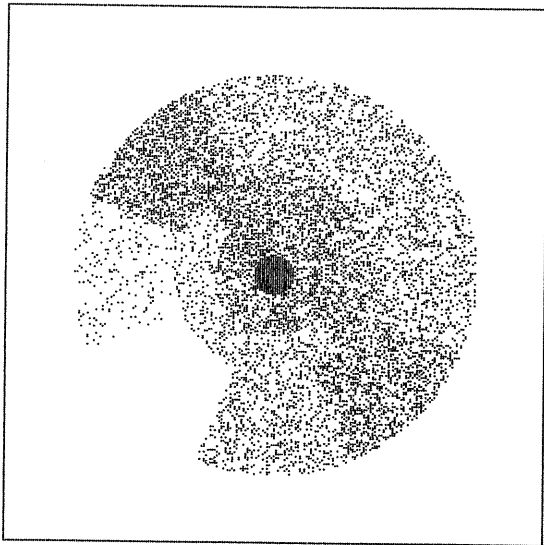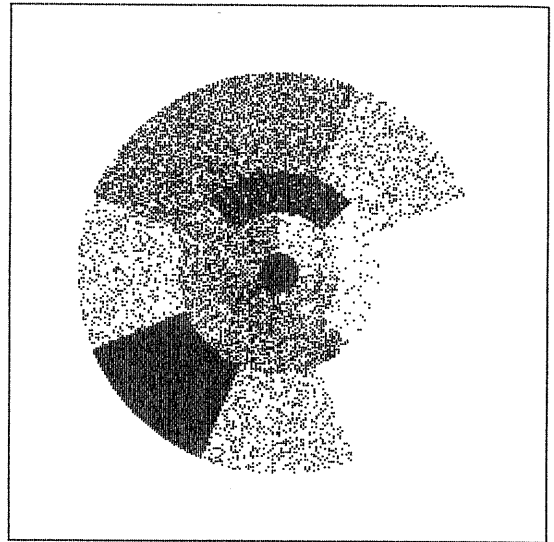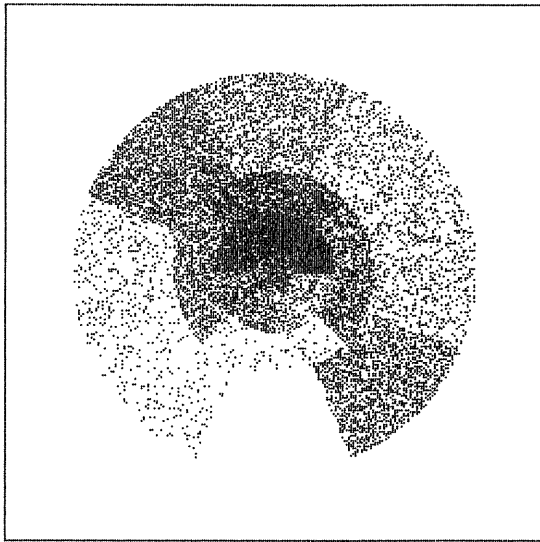
Figure 25

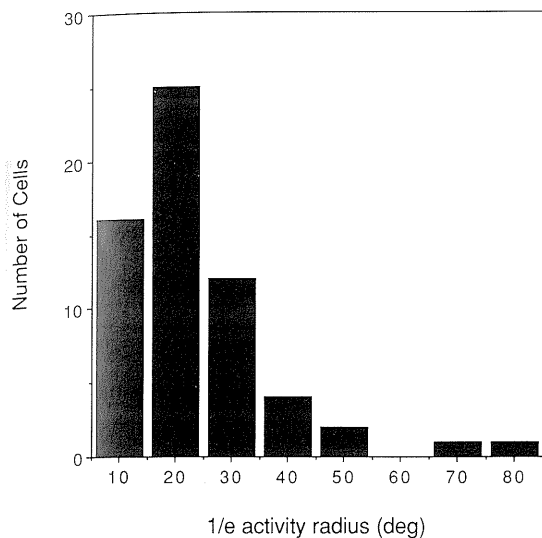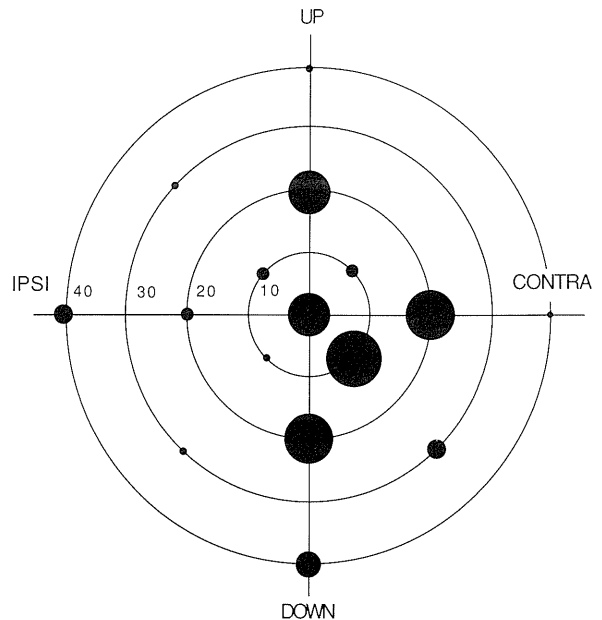## A) Receptive Field Radi

B) Receptive Field Centers

Fig. 26. **A:** Distribution of area 7a receptive field radi. The radius of each receptive field is the average length from the peak of activity to 37% (1/e) of the peak. **B:** Each dark circle is positioned on one of the 17 locations used to test light sensitivity in the visual field. The diameter of each dark circle is proportional to the number of receptive fields that had their peak response at that location.

'77; Mountcastle et al., '75) and Hyvarinen and colleagues (Hyvarinen and Poranen, '74; Leinonen et al., '79; Leinonen and Nyman, '79; Hyvarinen, '82). These investigators described neurons that had sensory-related responses to visual and somatosensory stimuli and that had behaviorally related responses to saccades, smooth pursuit eye movements, fixation, and reaching. Mountcastle et al. ('75) noted that there appeared to be some topographic organization for these properties since nearby cells tended to be of the same response class. Hyvarinen and Shelepin (Hyvarinen and Shelepin, '79; Hyvarinen, '81) mapped the functional organization of the inferior parietal lobule and reported visual and visuomotor functions to be located medially, whereas somatosensory and some visual activity was found laterally. Robinson and Burton ('80b,c) made extensive maps of the lateral inferior parietal lobule (area 7b) and found 80% of the cells to be responsive to somatosensory stimuli and the remaining cells to be either visual or visual and somatosensory. Although the somatosensory receptive fields were very large, some including most of the body, they reported a crude somatotopic organization.

The classification of many parietal cells as being motor-related was criticized by Robinson et al. ('78) when they found that nearly all cells in their recording experiments from area 7 had either visual or somatosensory responses. They argued that the seemingly behaviorally related responses could arise from sensory stimulation either from the target of a movement or as a result of the movement. For instance, a saccade-related response may be the result of either stimulation by the target for the saccade, or by the visual background of the test chamber stimulating the retinas as the eyes move. In subsequent experiments that were designed to separate visual from eye movement related responses Sakata and colleagues (Sakata et al., '83) showed smooth pursuit activity and Andersen and colleagues (Andersen et al., '87; Andersen, '87; Andersen and Gnadt, '89) showed saccade and fixation activity in the absence of any visual stimuli. Parietal cells also change activity when the animal is required to fixate through prisms of different diopter values; under these conditions the eye position changes, but the retinotopic positions of all visual inputs remain constant (Andersen et al., '87). Andersen and colleagues (Andersen, '87; Andersen et al., '87; Zipser and Andersen, '88) also showed that most fixation cells under these controlled conditions had "gaze" fields, the property first observed by Lynch et al. ('77) that the activity of the fixation cells varied as a function of the position of the eyes in the orbits. As a result, Andersen et al. ('87) labelled the activity of these cells as *eye-position* related.

In the functional mapping experiments reported here, the special fixation and saccade tasks are used to evaluate eye-position- and saccade-related responses under conditions in which visual stimulation could not be a factor. Also, the visual receptive fields were quantitatively mapped with the animal steadily fixating a fixation point, giving a precise

Fig. 25. Six representative visual receptive fields recorded from area 7a neurons. Each cell is tested with 500 msec light flashes at 17 locations in the visual field. Sectors centered on each test position are shaded proportional to the peak activity with the darkest sector representing the highest activity. The diameter of the total illustrated circular area is 100° of visual angle. Rates of highest evoked activity for these cells are **upper left,** 31.1 spikes/sec; **upper right,** 17.8; **middle left,** 17.6; **middle right,** 23.8; **lower left,** 18.0; **lower right,** 43.4.
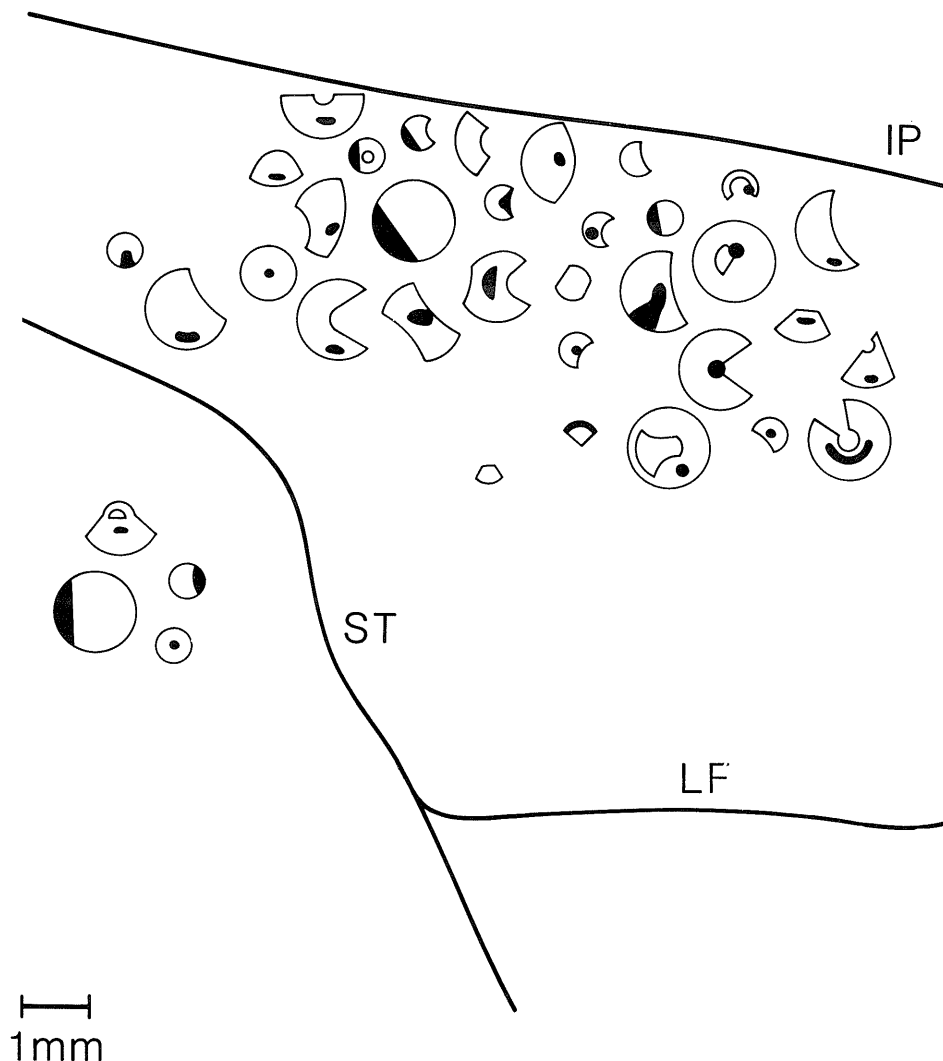
Fig. 27. Topographic organization of receptive fields in area 7a. The receptive fields are organized according to the location on the cortical surface of the electrode penetration from which they were recorded. All recordings above the superior temporal sulcus (ST) were made in area 7a. The dark part of each receptive field indicates the location of its peak activity. The total diameter of the largest receptive fields is 100°.

indicator of the visual sensory properties of the inferior parietal lobule neurons. A clear regional variation for somatosensory and visual responses was found with visual activity being found in areas 7a, LIP, and DP of the medial aspect of the lobule and somatosensory responses laterally in area 7b. Areas 7a, DP, and LIP had eye-position- and saccade-related activities. Area LIP was found to contain a large proportion of neurons showing presaccadic activity, whereas 7a and DP neurons gave postsaccadic responses. Within areas 7a and LIP, saccade- and eye-position-related activity was regionally intermixed. Area 7a had larger receptive fields than areas LIP and DP, which were usually bilateral. It was not uncommon to find area 7a neurons with receptive field peaks in the ipsilateral visual field, whereas this was rare for area LIP and DP neurons. Area DP neuron receptive field centers were generally confined to the lower visual field.

Relationship of anatomical and functional subdivisions

Of particular interest is the correlation of the functional organization of the inferior parietal lobule with its anatomical subdivisions. The experiments in this study give further evidence for a functional subdivision of the inferior parietal lobule. At the first level of subdivision the medial aspect of the lobule appears to be involved in visual and visuomotor functions, whereas the lateral aspect of the lobule appears to be specialized for somatosensory and somatomotor functions. The medial, visual area can be further subdivided into three areas: area LIP, which plays a role in the processing of saccadic eye movements; area MST, which plays a role in motion perception and smooth pursuit eye movements; and area 7a, which appears to play a role in spatial perception.

The anatomical experiments of this study provide further

Fig. 28. Proposed hierarchy for the flow of visual information into area 7a based on the laminar distribution of sources and terminations of the projections. Dotted lines represent connections that are of the *mixed* or *intermediate* type. The boldface square encompasses those fields in the posterior parietal cortex and adjoining dorsal aspect of the prelunate gyrus.

Fig. 29. Proposed hierarchy for the connections of areas 7a, 7b, LIP, and DP with other cortical areas. The connections with extrastriate areas shown in Figure 26 are excluded in this figure.

evidence that the posterior parietal cortex can be subdivided on connectional grounds. In particular, area 7a appears to be very different from the other visual areas in the inferior parietal lobule in that it is the only area that connects to some of the highest centers of the brain including the cingulate gyrus, large areas of the parahippocampal gyrus, the presubiculum, area PGm, and the rostral superior temporal sulcus, including the inferotemporal cortex. This last connection is a particularly important one, since it represents a direct connection between the area thought to be most crucial for object perception (inferotemporal cortex) and the area most crucial for spatial perception (the posterior parietal cortex).

The finding of a convergence of eye position and visual information in area 7a suggests that it might play a role in spatial perception. In fact, the nature of this convergence is consistent with the distributed representation for spatial locations that result with a model for computing spatial location in a parallel network (Andersen et al., '85b; Zipser and Andersen, '88; Andersen and Zipser, '88). The finding that the saccade responses begin at the initiation of or during saccades suggests that this activity may be an efference copy and lends additional support to the possible spatial-perceptual role of this region. Lesions with ibotenic acid restricted to area 7a (Bock et al., '87) or cooling this region (Stein, '78) produce spatial inaccuracies in reaching movements in monkeys.

Area LIP has a great deal of saccade-related activity and has strong connections to other saccade centers in the brain. In particular, it is the area of the inferior parietal lobule that projects most strongly to the frontal eye fields. It is also the area that has the strongest projection to the superior colliculus. Electrical stimulation thresholds for evoking saccadic eye movements are lower for area LIP than for area 7a (Shibutani et al., '83).

Andersen and Gnadt ('89) and Gnadt and Andersen ('88) have reported that 48% of the area LIP cells they sampled were saccde related in tasks that separated saccade from visual responses. Forty-three percent of these saccade-related cells were presaccadic. These results are compared to the data from area 7a in which only 28% showed true saccade responses in the control experiments and none of these cells were presaccadic. These data suggest that area LIP may have a more direct role in processing saccades than area 7a. Also Gnadt and Andersen ('88) found cells in area LIP that have memory-related activity in delayed saccade tasks in which the animal must memorize the location of a saccade target and withhold a saccade for varying amounts of time. These cells are direction and amplitude tuned. Special double saccade experiments showed that this memory linked activity was coding in motor, and not sensory, coordinates. Therefore this activity is related to the *intent* of the animal to make an eye movement of a specific amplitude and direction. This intentional activity and the presaccadic nature of the saccade responses suggest that area LIP may play an important role in processing saccadic eye movements. It is interesting to note that the intended movement activity found in cells in area LIP is very similar

if not identical to the activity recorded from the quasi-visual cells by Mays and Sparks ('80) in the intermediate layer of the superior colliculus, the layer of the colliculus to which area LIP projects.

Cells in area MST have large receptive fields and are generally motion sensitive. The visual motion properties of area MST neurons appear to be more elaborate than those of area MT which projects to MST. Area MST neurons have been reported to respond to the complex structure of velocity fields including neurons that are selective to expansion or rotation (Sakata et al., '85; Saito et al., '86; Tanaka et al., '86). Area MST also appears to be the locus of neurons displaying smooth pursuit eye movement activity (Sakata et al., '83; Komatsu and Wurtz, '88; Newsome et al., '88). Interestingly, area MT also projects to the densely myelinated portion of area LIP and could represent a connection by which saccadic and tracking eye movements are coordinated during pursuit behavior.

Area 7b has largely somatosensory and somatomotor responses and is connected predominantly to somatosensory areas. On the other hand, all the medial parietal areas which are visual in nature connect to areas of the brain that are primarily visual. In particular, area 5 projects only to area 7b in the inferior parietal lobule, and this route probably represents one of the most direct pathways for somatosensory information to flow into the lobule. It is interesting to note that there is almost no overlap in the projections of area 7a and 7b with the exception of the cingulate, MST, and PGm; and even in the cingulate there appears to be some segregation in the regional strengths of connection. Unfortunately the important question of whether area 7a and 7b are connected was difficult to resolve in our material because of tracer diffusion at the injection sites of these two neighboring areas. Since 7a injections often produced labelling in 7b but not labelling in areas connected to 7b, it is likely that connections between 7a and 7b do exist.

It would be of tremendous interest to know if the connections of area VIP differ markedly from the connections of area LIP. If not, then a thorny question is whether area LIP and VIP should be considered different areas, based primarily on their difference in myelination. In our experiments we found area DP and 7a to project to LIP but not VIP. Ungerleider and Desimone ('86b), on the other hand, found area MT to project to both VIP and area LIP (which they called VIP*).

Criteria for defining a cortical field

Rose ('49) originally proposed three criteria for establishing a cortical field: that it should be unique in terms of cytoarchitecture, connections, and function. Since this time additional criteria have also been used, including topographic representation (for example, a retinotopic map), myeloarchitecture, and other histological staining differences. The areas discussed in this paper have at least been distinguished on the basis of connection and, as listed below, on the basis of myeloarchitectural and cytoarchitectural differences. Many have also been defined on functional and topographic criteria (see Van Essen, '85, for review). However, the borders between many areas are difficult to define precisely. The only exceptions are area VI and, to a lesser extent, areas V2 and MT (Van Essen, '85; Hubel and Livingstone, '87). Another problem is that some currently recognized areas are heterogeneous for certain properties. For instance, areas MT and MST are heterogeneous for myelin staining, as discussed by Ungerleider and Desimone

('86). As indicated from the data outlined in the results, so is area LIP. Area LIP also contains one difference in connections; area MT projects to the myelinated aspect of LIP but not to the unmyelinated part (Ungerleider and Desimone, '86b; Blatt et al., '90). On the other hand, the remaining 12 other connections are the same for the two areas, and the physiological responses are undistinguishable between the two areas (Blatt et al., '87, '90; Gnadt and Andersen, '88).

Based on the connectional and myeloarchitectural distinction, we have further divided area LIP into two subdivisions (Blatt et al., '90). Area LIPd is the less myelinated, dorsal aspect of LIP, which is not connected to area MT, and area LIPv is the ventral aspect of LIP, which is more heavily myelinated and is connected to area MT. Based on the similarities of the other connections and physiological properties, we have maintained the designation of area LIP for the two subregions. It has generally been our approach not to subdivide areas into many very small cortical fields based on staining or patterns of connections. For instance, should the blob regions of VI be considered a separate cortical field from the interblob regions of VI since they have physiological, histological and connectional differences? What about the thick, thin, and interstripe areas of V2? Of course, if more evidence accumulates for differences between the heavier (LIPv) and lighter myelinated (LIPd) portions of area LIP, then this area will likely be reclassified as two cortical fields.

Relation of current findings to previous work

The connections of areas DP and LIP have not been previously studied, and the experiments reported here represent the first detailed accounting of the total projection patterns of these two areas. Several laboratories have studied the connections of area 7. However, our experiments differ from many of the earlier experiments in that previous studies generally used large injections of tracer or large lesions and were not concerned with delineating subdivisions within area 7 (Pandya and Kuypers, '69; Divac et al., '77; Mesulam et al., '77; Hedreen and Yin, '81). In more recent experiments smaller injections have been made in area 7 with the idea of delineating subdivisions within this region (Stanton et al., '77; Pandya and Seltzer, '82; Neal et al., '87, '88a). The experiments reported here represent an elaboration and extension of these studies, since they incorporate the most recent parcellations of extrastriate cortex (Van Essen, '85; Ungerleider and Desimone, '86a,b; Colby et al., '88; Zeki and Shipp, '88) and the inferior parietal lobule (Andersen, '87) and also report several new connections. In our experiments we have used very small injections of anterograde and retrograde tracers, combined in three hemispheres with functional mapping, to delineate functionally and anatomically two subdivisions within area 7, areas 7a and 7b. A more detailed account of the relation of our findings to previous studies for areas 7a, 7b, DP, and LIP follows.

Area 7a. One of the most important findings of this study has been the delineation of the multiple sources of visual input into area 7a derived from extrastriate cortex. While a good deal of knowledge has been obtained regarding the interconnections of striate and extrastriate cortical areas including areas V1, V2, V3, V3A, V4, MT (or V5), PO, and MST (Van Essen, '85; Ungerleider and Desimone, '86a,b; Zeki and Shipp, '88; Colby et al., '88) involved ir earlier stages of visual processing, it has not been wel

understood how area 7a is anatomically related to these earlier visual areas.

In the present study it was found that area 7a receives inputs from both areas DP and LIP, which were in turn found to receive inputs from several of the extrastriate areas, including V4, PO, and V3A to DP and MT, MST, V4, and PO to LIP. A connection of the caudal gyral surface of the inferior parietal lobule (area 7a) with the dorsal prelunate gyrus (Area DP) has not been reported in previous connectional studies, possibly because many of these studies employed large injections of tracer with resulting large injection sites that may have masked this local connection. Pandya and Seltzer ('82) did find a projection from their area Opt to the general region of area DP. These investigators divided the general region labelled area 7a in this study into two regions, a more caudal area Opt and a more rostral area PG. Based on our anatomical and functional mapping data we did not find it necessary to divide area 7a into two regions. In degeneration studies Kuypers et al. ('65) and Pandya and Kuypers ('69) noted a projection from the prelunate gyrus to the surface of the caudal inferior parietal lobule.

Interestingly, a projection from the lateral intraparietal sulcus (area LIP) to the gyral surface of the caudal inferior parietal lobule (area 7a) or from this area to the lateral intraparietal sulcus was not found in previous studies (Pandya and Seltzer, '82; Neal et al., '88a). The reason for this discrepancy is not clear.

Area 7a was also found to receive direct inputs from area MST, and area PO. Our anterograde tracing experiments confirm the area 7a to PO projection found by Colby et al. ('88) after injections of retrograde tracer in area PO. Although several investigations had found anterograde or retrograde label in the anterior bank of the superior temporal sulcus in the general region of area MST after area 7a injection, this is the first study to establish this connection directly to the physiologically defined area MST using the myeloarchitectural criteria established by Ungerleider and Desimone ('86a). Neal et al. ('88a) reported projections from areas MST, V4, V2, PO, and V3 to area 7a. The findings of efferent projections from areas V4 and V3, which were not found in this study, appear to be due to the fact that they considered area LIP to be part of area 7a. Area LIP receives a projection from V4 and V3; however, no connection of area LIP or area 7a with V2 was found.

It is interesting to note that the posterior parietal cortex of the owl monkey, a new world monkey, also receives visual inputs from several extrastriate cortical areas. Kaas et al. ('77) found inputs to the posterior parietal cortex arising from the dorsomedial area, medial area, dorsolateral area, and MT; all established visual areas in the owl monkey.

Several laboratories have reported extensive connections between the caudal inferior parietal lobule and the superior temporal sulcus (Pandya and Kuypers, '69; Divac et al., '77; Mesulam et al., '77; Seltzer and Pandya, '78, '84; Hedreen and Yin, '81; Neal et al., '88a,b). We found reciprocal connections for area 7a with areas MST, FST, STP, and TE within the sulcus. The label in area TE is within the fundus and posterior bank of the rostralmost aspect of the gyrus and is contained within the inferotemporal cortex. Label in this general area has also been reported by Neal et al. ('88b). Perrett et al. ('82) and Desimone et al. ('84) reported cells responsive to faces in this very area. This projection is the only direct link between the dorsal visual pathway within the posterior parietal cortex and the ventral visual pathway

within the inferotemporal cortex. Since lesions and recording data implicate the posterior parietal cortex in spatial functions and the inferotemporal cortex in object recognition Ungerleider and Mishkin ('82) labelled the dorsal visual pathway the "where" system and the ventral visual pathway the "what" system. Thus the area 7a-inferotemporal reciprocal projection is of great theoretical importance since it represents the only direct connection between the two endpoints of the "what" and "where" pathways. This fact was also emphasized by Neal et al. ('88b). However, earlier levels of these two systems also communicate with each other. For instance, from the work of Seltzer and Pandya ('80, '84) and our own experiments, it is known that area V4 is reciprocally connected to the posterior bank of the intraparietal sulcus (area LIP). Area V4 is the major source of visual input to the inferotemporal cortex and likewise the present experiments have demonstrated that area LIP provides direct inputs to area 7a. Area MT, which appears to be even lower in the visual hierarchy of the "where" pathway than area LIP, also has connections with area V4 (Maunsell and Van Essen, '83; Ungerleider and Desimone, '86b). Similarly, we found area DP to be connected with area V4. Thus the dorsal and ventral visual pathways that make up the "where" and "what" systems are extensively connected at several stages.

Our double label experiments for the first time provide a direct comparison of the associational projections from the superior temporal sulcus to the prefrontal cortex and to area 7a. Although the projection pattern for area 7a is very extensive, the projections to the prefrontal cortex are even more widespread, including practically all the cortex within the sulcus. In all the experiments of this study area 7a was never found to be connected to area MT, whereas the prefrontal cortex was. Very few cells were double labelled in the superior temporal sulcus, indicating that the two projection populations, although spatially intermixed, are largely separate at the single cell level. Both projection patterns were discontinuous, but no systematic spatial relationship between the two populations was readily apparent. Thus this pattern of organization is similar to the relationship of area 7a populations projecting callosally to the contralateral area 7a and ipsilaterally to the prefrontal cortex (Andersen et al., '85a).

The reciprocal projections from area 7a to the prefrontal cortex are well documented (Pandya and Kuypers, '69; Pandya et al., '71; Chavis and Pandya, '76; Divac et al., '77; Mesulam et al., '77; Stanton et al., '77; Jacobson and Trojanowski, '77; Leichnetz, '80; Barbas and Mesulam, '81, '85; Petrides and Pandya, '84). In these studies projections to and from area 7a were found in the periarcuate cortex anterior to the fundus of both the superior and inferior branches of the arcuate sulcus and in the cortex in and around the principal sulcus. These cortical areas correspond to areas 45, 8a, and 46 of Walker and are the regions found to connect to area 7a in this study. We also found light labelling in the supplementary eye fields of Schlag and Schlag-Ray ('86) anterior to the supplementary motor field and in area 11 of Walker in the orbital prefrontal cortex.

We further found that with restricted injections of tracer confined entirely or almost entirely to area 7a that the label in the prefrontal cortex was strongest in area 46. This contrasts with our further findings that area LIP projects most strongly to area 8a and area 7b to areas 45 and area 6. Area 8a contains a good deal of the frontal eye fields.

Extensive reciprocal projections were seen on the medial surface of the hemisphere that began at the occipito-temporal sulcus and extended continuously through the retrospenial area, area PGm of Pandya and Seltzer ('82) to both the posterior (area LC) and anterior (area LA) aspects of the cingulate gyrus. This general projection has been noted in several studies (Pandya and Kuypers, '69; Mesulam et al., '77; Baleydier and Mauguiere, '80; Pandya et al., '81; Hedreen and Yin, '81; Seltzer and Pandya, '84; Neal et al., '88a). There are strong connections with area PO confirming the observation of Colby et al. ('88) of a projection from area 7a to PO. Area PO is a visual extrastriate area which contains a retinotopic map of the contralateral visual field that emphasizes the periphery more than most other visual cortical fields (Gattass et al., '85; Colby et al., '88). Area PO is located in the ventral aspect of the anterior bank of the parieto-occipital sulcus and extends out of the sulcus and onto the medial wall of the hemisphere. Area PO may be homologous to area M in New World monkeys (Colby et al., '88). Although extensive labelling was seen in PO after 7a injections, label extended beyond the borders of PO into many neighboring regions. These areas included the posterior intraparietal area (PIP), located in the fundus of the intraparietal sulcus and medial intraparietal area (MIP), located dorsal and anterior to PO in the medial bank of the intraparietal sulcus. These areas have been defined by Colby et al. ('88) on the basis of myeloarchitecture and connections with area PO. Label was also seen in cortex dorsal to area PO both within the sulcus and on the medial wall of the hemisphere. Some of this area was originally included in area PO by Gattass et al. ('85), but was later determined by Colby et al. ('88) to be a separate area. They noted that this region stained lighter for myelin than PO, that the cells in this region gave weaker visual responses than in PO, and that this region had several different inputs from PO receiving projections from the cingulate gyrus and the crown of the prelunate gyrus (probably area DP) and not receiving inputs from area V1. The aspect of this area that lies on the medial wall of the hemisphere Colby et al. ('88) labelled the medial dorsal parietal area (MDP).

The connections of area 7a with the cingulate were stronger for the more posterior area LC than the more anterior area LA. This was true for both the anterograde and retrograde labelling. Pandya et al. ('81) reported stronger projections to area 7a when anterograde tracer was injected in the posterior cingulate gyrus compared to the anterior cingulate gyrus consistent with our area 7a injection results. The labelling in the cingulate was very heavy, consistent with the observation of Mesulam et al. ('77), and it was of nearly equal strength to both hemispheres, confirming the observation by Hedreen and Yin ('81). Our data showed that the heterotopic callosal connections of area 7a, with the exception of the cingulate, were weaker than the ispilateral associational projections.

Strong connections with area TF in both banks of the occipito-temporal sulcus and up onto the surface of the parahippocampal gyrus were observed, consistent with the reports of Seltzer and Pandya ('76, '84), Mesulam et al. ('77), and Hedreen and Yin ('81). The anterior and more medial projection on the surface of the gyrus (TFm) was found to have a much different laminar pattern of connections for both anterograde and retrograde labelling compared to the more posterior and lateral projection (TFl) contained predominantly within the occipito-temporal sulcus. The ante-rior-medial area had a laminar pattern of labelling indicative of a presumed feedforward projection from area 7a, whereas the posterior-lateral pattern was more indicative of a presumed feedback projection. Seltzer and Pandya ('84) assigned terminal label in the parahippocampal gyrus after area 7 injections to three areas—a more lateral TF which likely corresponds to our more posterior lateral zone, and more medial areas TL (Rosene and Pandya, '83) and TH which may correspond to our more medial-anterior zone of label. Finally a projection from 7a to the presubiculum was found that was not reciprocal. This projection had been previously reported by Seltzer and Van Hoesen ('79) and Seltzer and Pandya ('84).

Seltzer and Pandya ('84) made the observation that the rostral surface of the inferior parietal lobule has almost no projections to the temporal lobe, whereas the caudal inferior parietal lobule has very extensive connections to areas in the superior temporal sulcus and parahippocampal gyrus. Our observations support theirs with the exception that we found projections from 7b to areas STP, MST, and TE of the superior temporal sulcus. Neal et al. ('88b) also reported projections to the ventral superior temporal sulcus from area 7b. Our subsequent experiments in area LIP and DP indicate that area 7a is unique among the other cortical areas in several other ways. Both areas DP and LIP differ from area 7a in having rather limited connections with the superior temporal sulcus connecting to areas located in only the caudal third of the gyrus. Area LIP does project to area TF and area 46, but these connections are much sparser than the ones observed for area 7a. Finally, neither of these other two cortical areas was found to be connected to the cingulate gyrus. Thus area 7a appears to be unique among the other visual cortical areas in the inferior parietal lobule in having strong connections to areas in the temporal lobe and cingulate gyrus that may be considered to be at the highest level in the hierarchy of cortical areas. This observation is consistent with the hierarchy of cortical projections proposed in this study based on the laminar distribution of labelling. This hierarchy has areas LIP, DP and MST feeding forward to area 7a. Also consistent with this hierarchical structure is the finding of Asanuma et al. ('85) that, whereas areas LIP and DP are reciprocally connected to the lateral pulvinar, area 7a is connected to the medial pulvinar. The medial pulvinar is also connected to several high-order cortical areas such as the cingulate, anterior superior temporal sulcus, and prefrontal cortex, whereas the lateral pulvinar is connected primarily to other extrastriate cortical areas.

Area 7b. Whereas the connections of areas 7a, LIP, and DP were found to be predominantly with visual cortical areas, the connections of area 7b included more somatosensory cortical areas. This pattern of connectivity fits with the recording data from area 7b, which indicates that its neurons have largely somatosensory- and somatomotor-related activity. This pattern also fits with the subcortical projections of area 7b; it connects primarily to the oral division of the pulvinar, which is also connected to area 5, a major somatosenory association area (Asanuma et al., '85), and it projects to pontine nuclei that receive extensive input from motor and premotor cortical areas (May and Andersen, '86). Areas 7a, LIP, and DP, on the other hand, connect to different areas of the pulvinar and pontine nuclei that generally overlap with connections from other visual areas. In our experiments we found area 7b to be reciprocally

connected to areas 5, PGm, PO, MST, STP, TE, the cingulate gyrus, areas 45 and 6 in the frontal lobe, and area Ig in the insula.

Previous reports of connections of area 7 within the parietal lobe have focused on the connections between areas 5 and 7 (Jones and Powell, '70). Consistent with the results of our experiments, other investigators have found area 7b to be the only source of direct connections between the inferior parietal lobule and area 5. Caminiti and Sbriccoli ('85) found anterograde and retrograde label restricted to area 7b after injections of HRP in area 5. Using anterograde autoradiographic and ablation tracing techniques, Pandya and Seltzer ('82) showed that the superior parietal lobule projects to the rostral but not the caudal aspect of the surface of the inferior parietal lobule. Neal et al. ('86, '87) reported label in area 5 only after injections in area 7b and not after injections in area 7a. As with our experiments, they found all regions of area 5 to connect to area 7b, including the medial bank of the intraparietal sulcus and the surface of the superior parietal lobule.

Connections to other areas of the parietal cortex have been less well elucidated. Colby et al. ('88) reported a projection from the surface of the inferior parietal lobule to area PO, but they did not distinguish between areas 7a and 7b. Pandya and Seltzer ('82) do not report connections between area PGm on the medial wall of the hemisphere and 7b but labelling in the general region of 7b and 7a can be seen in their Figure 5 after injection of anterograde tracer in area PGm.

It is also not clear if there are direct connections between areas 7a and 7b. Neal et al. ('86) claim that these two areas are not interconnected; however, Pandya and Seltzer ('82) trace a cascade of connections between the rostral and caudal aspects of the inferior parietal lobule. Unfortunately in our experiments local tracer diffusion made it difficult to evaluate this connection; however, labelling in either of the areas after injection in the other was usually not strong.

Seltzer and Pandya ('80, '86) reported a projection from area 7b to the anterior aspect of the lateral bank of the intraparietal sulcus. Our tracing experiments confirm these results. The area of labelling is located anterior to area LIP. In our recording experiments, on the occasions where the electrode entered this region, we recorded somatosensory fields. These observations raise two possibilities: 1) that area 7b continues from the surface of the inferior parietal lobule into the anterior part of the intraparietal sulcus or 2) that this area is a separate cortical field from areas 7b or LIP that receives input from area 7b. Robinson and Burton ('80b) in their mapping studies of area 7b recorded from the lateral fissure and surface of the inferior parietal lobule but did not record within the intraparietal sulcus. From their maps of the area one would expect that the face should be represented in the intraparietal sulcus if this region is a continuation of the somatotopic map of area 7b.

Several investigators have reported connections between area 7b and area SII (Stanton et al., '77; Pandya and Seltzer, '82; Neal et al., '87). We saw this connection when injections of tracer were made anteriorly in area 7b but not when they were made posteriorly in 7b. One interpretation would be that the labelling in area SII is due to spillage of tracer into SII; another would be that only the anterior aspect of area 7b and SII are interconnected (e.g., the hand region).

Both our data and those of Seltzer and Pandya ('78, '84) indicate that area 7b is connected with the anterior bank of the caudal third of the superior temporal sulcus. Seltzer and Pandya labelled this area TPO; our data indicate that this projection includes the densely myelinated zone (DMZ) and therefore includes at least a part of area MST (Ungerleider and Desimone, '86a,b). Caminiti and Sbriccoli's experiments indicate that this general region also is interconnected with area 5. Neal et al. ('87) reported a connection of area 7b with the floor of the anterior third of the superior temporal sulcus. This area appears to overlap with the projection zone in STP and TE that we observed.

Our result of a projection from area Ig in the insular cortex restricted to area 7b confirms the reports of Mesulam and Mufson ('82b) and Neal et al. ('87). Whereas our injections into area 7a produced heavier labelling in the posterior aspect of the cingulate in area LC, injections into area 7b produced stronger labelling in the anterior aspect of the cingulate in area LA. A similar finding was made by Pandya et al. ('81). Also, our injections into area 7b produced a very different pattern of labelling in the frontal lobe compared to areas 7a, LIP, or DP with label concentrated in areas 45 and 6 of Walker. A similar distribution of label was found in the frontal lobe after injection of anterograde tracer into the rostral inferior parietal lobule by Petrides and Pandya ('84), although the parcellation they used of the frontal lobe was somewhat different than Walker's.

The above results indicate that area 7b has connections to areas PO, MST, STP, and TE; all of these areas are part of visual extrastriate cortex. Although area 7b has been found to be primarily a somatosensory area in recording experiments, it has been emphasized in several of these experiments that a small proportion of the cells in this region respond to visual stimuli (Mountcastle et al., '75; Robinson and Burton, '80b,c; Hyvarinen, '82). It is likely that these visual inputs are derived from areas MST, STP, TE, and PO.

Area LIP. Area LIP was first described by Andersen et al. ('85a) on the connectional criteria that this region has the strongest projections to the ipsilateral prefrontal cortex when compared to areas 7a and 7b. It made up a good deal of the posterior half of area POa. In Seltzer and Pandya's original description of area POa, they noted that the posterior half was connected primarily to visual areas, whereas the anterior half was connected primarily to somatosensory areas, consistent with our present suggestion that area POa spans at least two cortical areas. Experiments in which injections of anterograde and retrograde tracers were made into area LIP provided further evidence for it being a separate area from areas 7a and 7b on the basis of thalmocortical-corticothalamic connections and projections to the tectum and pons. Asanuma et al. ('85) found that area LIP has its principal thalamic connections with the lateral pulvinar nucleus, whereas area 7a connects primarily to the medial pulvinar and area 7b connects primarily to the oral pulvinar. Differences were also noted by Asanuma et al. ('85) between the areas for more minor connections to several other dorsal thalamic nuclei. Fries ('84), Asanuma et al. ('85), and Lynch et al. ('85) found that area LIP projects much more strongly to the intermediate layers of the superior colliculus compared to area 7a. Asanuma et al. ('85) found no projections to the intermediate layers from area 7b but did find projections to the deep layers and to the intercollicular region. Differences were also noted in the projections to the pretectum and ventral thalamus. May and Andersen ('86) observed differential projection patterns in

the pons for areas LIP, DP, 7a, and 7b. Interestingly, the corticopontine projection pattern for area LIP was very similar to the pattern found for the frontal eye fields (Kunzle and Akert, '77; Brodal, '79). The strong connections of area LIP with the frontal eye fields and intermediate layers of the superior colliculus are consistent with the functional observations that area LIP appears to play an important role in the processing of saccadic eye movements (Gnadt and Andersen, '88; Andersen and Gnadt, '89).

Area LIP was found to connect cortically to areas MT, MST, DP, PO, V3d, V3v, V3A, V4, 7a, and TEO of extrastriate cortex; to area TF in the parahippocampal gyrus; and to areas 46 and 8 of the prefrontal cortex. The overall pattern of corticocortical connections of area LIP had previously not been studied systematically by making lesions or injections of tracer directly into area LIP. However, studies of areas connected to area LIP provide supporting evidence for some of these connections.

Ungerleider and Desimone ('86b) found a projection from area MT to the heavily myelinated portion of area LIP but not to the smaller lightly myelinated portion. Colby et al. ('88) reported projections from area LIP to area PO. Seltzer and Pandya ('80, '86) reported projections from the prelunate gyrus in the general area of V4 to the general area of LIP in the caudal bank of the intraparietal sulcus. They also reported a projection from area PF (7b) to the rostral aspect of the bank. This observation is consistent with our finding that the cells in the cortex rostral to area LIP in the bank of the sulcus respond to somatosensory stimuli. Neal et al. ('88a) reported no connections between area 7a and LIP, inconsistent with our findings.

Using small injections of anterograde tracers into area 8a (frontal eye field) Kunzle and Akert ('77) found label in the inferior parietal lobule that was mainly concentrated in area LIP, consistent with our observation of relatively stronger connections of area LIP to area 8a compared to area 7a. Huerta et al. ('87) found heavy reciprocal labelling concentrated in area LIP after injection of HRP in the frontal eye fields. After large injections of retrograde tracer in area 46 Jacobson and Trojanowski ('77) found some labelled cells in the general area of LIP. Schwartz and Goldman-Rakic ('84) found labelled cells in a large number of areas in the prefrontal cortex, including areas 8a and 46 after large and multiple injections of retrograde tracer into the lateral bank of the intraparietal sulcus.

An important question is the degree to which the connections of area VIP vary from those of adjacent area LIP. Since the connections of this area have not been studied, it is an open question whether this area should even be considered distinct from area LIP. At present it is known that, like area LIP, area VIP receives input from area MT (Maunsell and Van Essen, '83; Ungerleider and Desimone, '86b). Area VIP is less densely myelinated than the adjoining area LIP, and area V2 projects to VIP (Ungerleider and Desimone, '86a), whereas we did not find this connection in this study for area LIP. Also, in our experiments we found areas DP and 7a to project to LIP but not VIP.

Area DP. Maguire and Baizer ('84), in a microelectrode mapping study, described an area in the dorsal most aspect of the prelunate gyrus, extending into the anterior bank of the lunate sulcus that was not topographically organized and thus distinct from cortical subdivisions they described located more ventrally on the gyrus. Many of the cells were reported to have receptive fields that extended well into the ipsilateral visual field. Asanuma et al. ('85)

named this area the dorsal prelunate area in experiments examining the subcortical connectivity of this region. Although they found that areas LIP and DP had differences in their subcortical connections, there were also major similarities that these two fields did not share with areas 7a and 7b. These included similar patterns of connection with the lateral pulvinar, zona incerta, pregeniculate nucleus, anterior pretectal nucleus, and superior colliculus. The finding that these two areas were also directly connected by reciprocal corticocortical projections (Andersen et al., '85a) suggested that they were functionally related in some important way. Andersen et al. ('85a) also reported connections between area 7a and DP and noted that area DP represented a potential source of visual input to area 7a. Van Essen ('85) reported that area DP receives inputs from VP (V3v) and V4. May and Andersen ('86) found the projection from area DP to the pontine nuclei to be weaker than the contributions coming from areas LIP, 7a, and 7b. This observation was consistent with the report of Glickstein et al. ('80, '85) that labelling in the dorsal prelunate gyrus was much weaker than labelling in the intraparietal and superior temporal sulci following retrograde tracer injections into the dorsolateral pontine nuclei. A weak projection from DP to area PO was reported by Colby et al. ('88), confirming our similar observation.

CONCLUSIONS

We have shown the sources of visual input to the inferior parietal lobule and have constructed a hierarchy of visual information flow into this region based on laminar patterns of connection. A broader hierarchy is also proposed that relates the positions of areas 7a, 7b, LIP, and DP to various cortical fields in the parietal, temporal, and frontal lobes. By combining single cell recording techniques in trained monkeys with anatomical tracing techniques we have parcelled the inferior parietal lobule into several subdivisions based on both anatomical and functional grounds.

From the results of this study there emerges the idea of a complex and highly distributed network, with each cortical area serving as a node in this network. An important next step is to understand the different processing functions being performed at each of these nodes.

ACKNOWLEDGMENTS

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