

■シンポジウム 後方連合野への新しい視点

Organization of the Posterior Parietal Cortex in Monkeys

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Since the publication of Critchley's *Parietal Lobes* in 1953, much work has been conducted to identify the neural substrates underlying the striking spatial neglect that follows lesions of the parietal lobule. The present chapter is intended to provide a brief overview of the anatomical organization of this enigmatic cortical region, and is based primarily on experimental data collected in monkeys.

The importance of the posterior parietal cortex in the hierarchical path for information arising in the somatic sensory cortex, and eventually entering the temporal lobe, was identified experimentally in the 1960's on the basis of axonal degeneration studies in macaque monkeys (Jones and Powell, 1970). Jones and Powell made a systematic series of localized lesions starting in each of the three primary sensory areas of the cortex and found that in the case of the somatic sensory system, lesions of areas 3b, 1 and 2 of the primary somatic sensory cortex result in degenerating axonal profiles within area 5 of the superior parietal lobule. When lesions were made in area 5, label appeared within the inferior parietal

lobule, and lesions of the inferior parietal lobule, or area 7, resulted in extensive axonal degeneration in the cortex lining the superior temporal sulcus.

A similar systematic flow of sensory signals into the cortex on the banks of the superior temporal sulcus occurs following lesions of the visual areas of the occipital cortex, as well as following lesions starting in the auditory cortex along the ventral bank of the lateral sulcus. Although a principal theme to emerge from the Jones and Powell study is the idea that the hierarchical flow of information originating in each of the primary sensory areas eventually converges deep in the temporal lobe, more recent studies indicate that a significant amount of sensory signals are directed elsewhere within the cerebral cortex. For example, studies carried out in a number of laboratories over the past 15 years or so clearly indicate that although much visual information (especially information important in high level pattern recognition and form analysis) flows into the temporal lobe, a significant amount of visual information flows dorsally into the parietal cor

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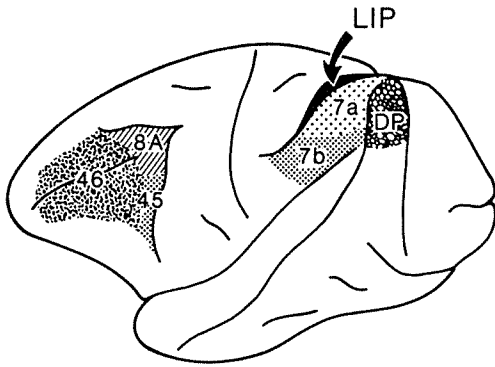


Figure 1

Schematic diagram illustrating the approximate locations of the major cortical areas involved in my anatomical studies. The identifications of the cortical areas are based in part on the cytoarchitectonic parcellation schemes established by Brodmann (1905) and by C. and O. Vogt (1919), and in part on anatomical connections and physiological properties.

tex as well.

My own anatomical studies of the inferior parietal lobule were initiated a number of years ago while I was a postdoctoral fellow in Dr. W. M. Cowan's laboratory at The Salk Institute for Biological Studies. Dr. Cowan and I conducted these experiments in collaboration with Dr. R. Andersen. In these studies, we examined the subcortical and intracortical interconnections of the inferior parietal lobule, which is at the confluence of the somatic sensory hierarchical pathway and the visual hierarchical pathway (Andersen et al, 1985, 1990 ; Asanuma et al, 1985). This cortical region, of course, had been shown to be crucial for neural operations involving somatomotor and visuomotor functions within extrapersonal space (Mountcastle et al, 1975).

The cortical fields located within the inferior parietal lobule and some nearby cortical areas as well are identified in figure 1. The subdivision of the inferior parietal lobule into areas 7a and 7b is based on the

division of Brodmann's area 7 (1905) into two fields by C. and O. Vogt (1919). The dorsal half of Brodmann's area 19 is identified as the dorsal prelunate area (DP), and the large cortical expanse buried along the ventral bank of the intraparietal sulcus (see curved arrow) is identified as the lateral intraparietal area, or LIP. Ventral to the area 7a / DP junction within the depths of the superior temporal sulcus, are the middle temporal area (MT) and the medial superior temporal area (MST), both of which are strongly implicated in the detection of motion. The subdivisions of the dorsolateral prefrontal cortex are based on Walker's delineations (Walker, 1938).

The cortical areas described above have readily identifiable, and distinct anatomical connections with the subdivisions of the pulvinar complex within the dorsal thalamus. The primate pulvinar complex comprises four distinct components. These are the oral pulvinar nucleus (Pul. o.), the medial pulvinar nucleus (Pul. m.), the lateral pulvinar nucleus (Pul. l.), and the inferior pulvinar nucleus (Pul. i.). These components of the pulvinar complex, together with the lateroposterior nucleus (LP), constitute the lateral group of nuclei, which occupies a large, wing-like mass in the caudolateral sector of the dorsal thalamus.

The retrogradely transported fluorescent dyes, Fast Blue and Diamidino Yellow, as well as the autoradiographic method following injections of tritiated amino acids that are transported in the anterograde direction, were used to identify the thalamic relations of the inferior parietal lobule. Injections of these anterograde and retrograde tracers into area 7a, or the exposed gyral surface of the caudal portion of the inferior parietal lobule, results in a characteristic

pattern of anterogradely labeled corticothalamic axons or of retrogradely labeled thalamocortical relay neurons within the medial pulvinar nucleus (Figure 2). The axonal and/or cellular labeling within the medial pulvinar nucleus consistently appears in the form of two to three disk-like aggregates of label that are stacked in the dorsoventral dimension within the nucleus with relatively label-sparse zones in between. This thalamic region is not known to be in receipt of inputs from subcortical sites that clearly process visual information, such as the retina and the superficial layers of the superior colliculus. Projections into the medial pulvinar nucleus are known to arise in the deep layers of the superior colliculus (Benevento and Fallon, 1975; Benevento et al, 1977; Harting et al, 1980; Benevento and Standage, 1983), however, visual responses in the deep layers of the superior colliculus are rare (Mohler and Wurtz, 1976; Wurtz and Mohler 1976).

In contrast, injections of tracers into the rostral half of the inferior parietal lobule, or area 7b, results in dense thalamic labeling within the oral pulvinar nucleus (Figure 3). This thalamic labeling is distinct from the labeling seen following area 7a injections of tracers since it is located distinctly rostral to the medial pulvinar nucleus, and since the label spreads densely and diffusely throughout the oral pulvinar nucleus (Figure 3). Disk-like aggregates of labeling, such as those seen in the medial pulvinar nucleus following comparable injections of tracers into area 7a, are not detected in the area 7b/oral pulvinar nucleus interconnection. As in the case of the medial pulvinar nucleus, no subcortical pathway, clearly conveying visually-related information, has been established to project into the oral

pulvinar nucleus.

In contrast to the rostral two subdivisions of the pulvinar nucleus described above (i. e. the oral and medial pulvinar nuclei), the lateral and inferior pulvinar nuclei are well known to be in receipt of visually driven signals from the superficial layers of the superior colliculus and the retinorecipient layers of the pretectum (Campos-Ortega and Hayhow, 1972; Benevento and Fallon, 1975; Ogren and Hendrickson, 1976, 1979; Benevento et al, 1977; Harting et al, 1980; Ungerleider et al, 1983; Benevento and Standage, 1983). Extensive anterograde and retrograde labeling within the lateral pulvinar nucleus as well as some labeling of the medial pulvinar nucleus occurs following injections of tracers into the lateral intraparietal area (Figure 4) and into the dorsal prelunate area (Figure 5). Like the disk-like aggregates of medial pulvinar nucleus label seen following injections of tracers into area 7a, the labeling patterns within the lateral pulvinar nucleus are patchy following tracer injections into the lateral intraparietal area and following tracer injections into the dorsal prelunate area.

In the course of our studies, we examined the thalamic relations of the lateral prefrontal cortex and compared this relation with the thalamic relations of the inferior parietal lobule. Injections of the retrogradely transported fluorescent dyes were made into the granular prefrontal cortical areas 8a, 45, and 46, rostral to the arcuate sulcus (see Figure 1). When the thalamic labeling resulting from these prefrontal cortex injections of dyes was examined, numerous retrogradely labeled neurons were found within the mediodorsal nucleus, the principal thalamic relay upon the prefrontal cortex. In addition, however, a distinct population

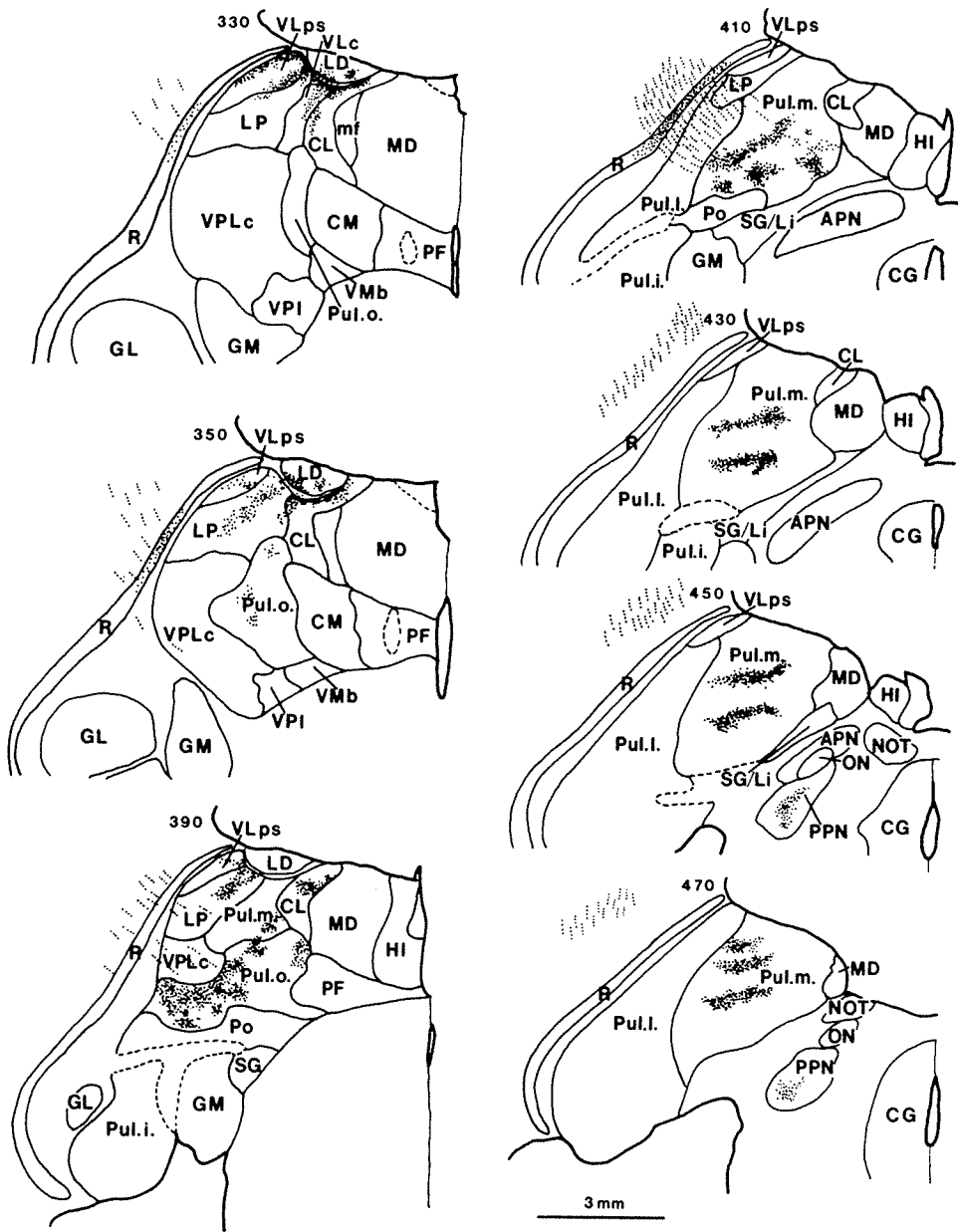


Figure 2

Frontal sections through the thalamus illustrating the distribution of anterogradely transported label within the thalamus following multiple injections of tritiated amino acids directed into area 7a. Although the bulk of the injection was made into area 7a in this case, there was some spread of the injection into areas 7b and 5a well, and disk-like aggregates of anterograde label are prominent in Pul. m. Rostralmost section is at top left, and caudalmost section is at bottom right in this and subsequent figures. The nomenclature and the abbreviations used to identify thalamic nuclei in figures 2 through 5 are derived from Olszewski (1952).



Figure 3

Frontal sections drawings through the thalamus showing the distribution of axonal arborizations arising in the rostral inferior parietal lobule. The injection was directed into area 7b, but involved SII and the rostralmost portion of area 7a as well. Thalamic labeling is densest in Pul. o. following area 7b injections of tracer.

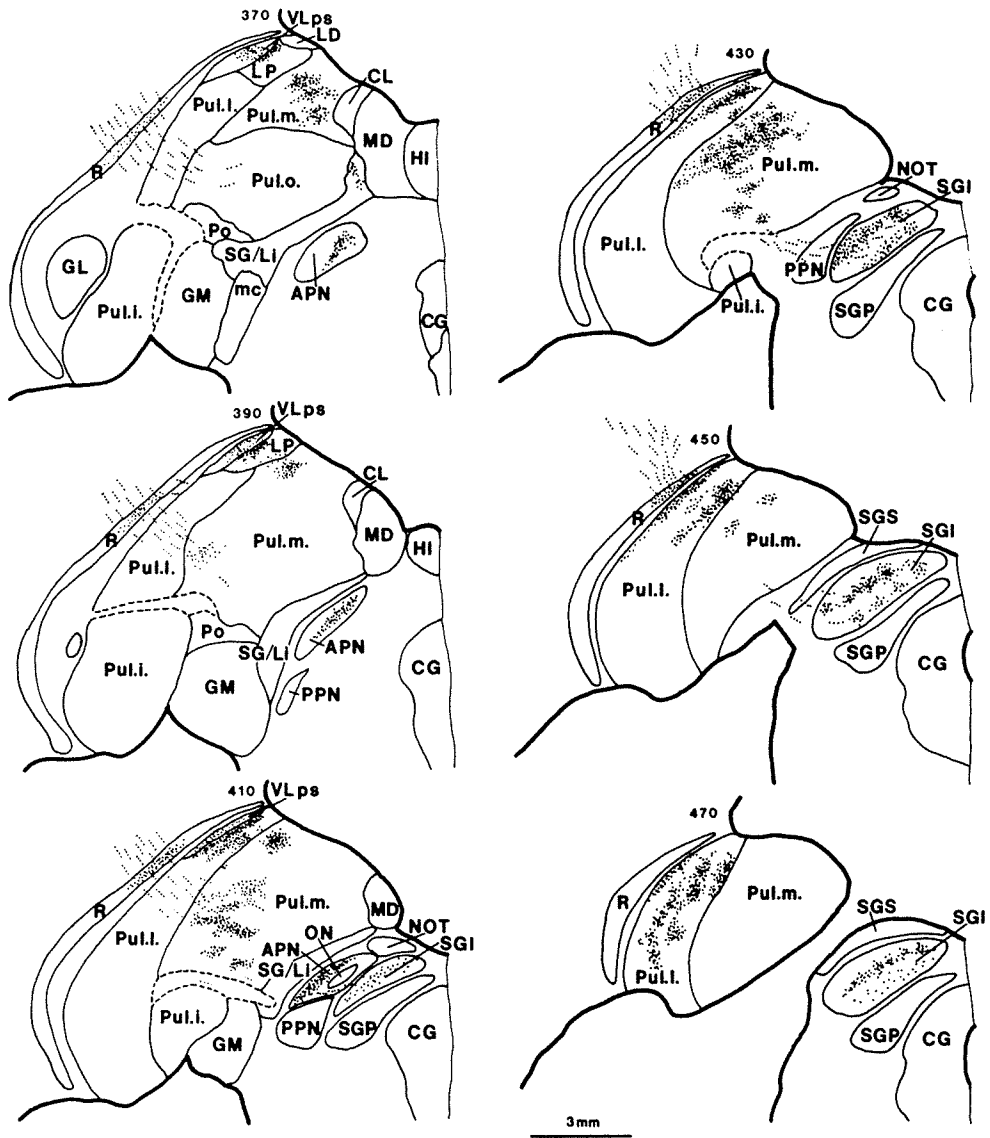


Figure 4

Illustrations of frontal sections through the thalamus showing anterograde labeling extending from the medial pulvinar nucleus into the lateral pulvinar nucleus, when injections of tritiated amino acids are directed into the lateral intraparietal area.



Figure 5

Dense anterograde labeling in the lateral pulvinar nucleus (in addition to labeling in the medial pulvinar nucleus) occurs also following injections of tritiated amino acids into the dorsal prefrontal area. Frontal Sections.

of neurons was observed within the medial pulvinar nucleus. Disk-like aggregates of medial pulvinar neurons projecting upon the prefrontal cortex, similar in size and orientation to the disk-like aggregates of neurons within this nucleus projecting upon area 7a, extended throughout much of the

rostrocaudal extent of the medial pulvinar nucleus.

To further our understanding of the relation of medial pulvinar nucleus neurons projecting upon the posterior parietal cortex with those projecting upon the lateral prefrontal cortex, we proceeded to make large

injections of a blue dye into the inferior parietal lobule, and large injections of a yellow dye into the lateral prefrontal cortex in the same hemisphere of one monkey. When the two distinctly labeled populations of neurons were examined in the same thalamic sections, it became apparent that instead of interdigitating, these distinct populations of thalamocortical relay neurons (projecting to different cortical lobes) occupied overlapping territories within the medial pulvinar nucleus, with the cell-sparse zones between the disks remaining relatively label-free even following these two large injections. Instead of overlapping completely, however, the cells projecting upon the prefrontal cortex tend to be located more medially than the cells projecting upon the inferior parietal lobule.

Taken all together these data indicate that area 7a is interconnected with the medial pulvinar nucleus, and that area 7a differs from area 7b, which is interconnected with the oral pulvinar nucleus. Both areas 7a and 7b are distinct from the lateral intraparietal area and from the dorsal prelunate gyrus, since these latter cortical areas are densely interconnected with the lateral pulvinar nucleus as well as with the medial pulvinar nucleus. The lateral intraparietal area and the dorsal prelunate gyrus are well poised to be in receipt of subcortically generated visual signals, whereas areas 7a and 7b are not.

In other studies not illustrated here, we examined some receptive field properties of neurons within each of the cortical fields we examined anatomically. Neurons in area 7b were primarily responsive to somatic sensory signals, whereas neurons in areas 7a, LIP and DP were responsive to visual signals. The visual receptive fields of neur-

ons within area 7a tended to be large and bilateral, whereas the receptive fields of neurons in the lateral intraparietal area and in the dorsal prelunate area (the cortical areas in receipt of input from the lateral pulvinar nucleus) were smaller and contralateral. Finally, neurons responsive to saccades and to eye position related signals were dispersed throughout area 7a, the lateral intraparietal area, and the dorsal prelunate area.

The intracortical interconnections of the cortical fields of the inferior parietal lobule follow also, the general principles that emerged from the thalamic studies. A good example of this was found in the organization of the dense interconnection of the posterior parietal region with the lateral prefrontal cortex.

Injections of anterograde or retrograde tracers in area 7a, for example, result in anterograde and retrograde labeling of the prefrontal cortex, primarily within the depths of the principal sulcus, within area 46 of Walker (Figure 1). In contrast, injections in area LIP result in reciprocal labeling of axonal arborizations and of retrogradely labeled neurons in area 8a along the dorsal bank of the arcuate sulcus (Figure 1), and, injections in area 7b result in anterograde and retrograde labeling within area 45, along the ventral bank of the arcuate sulcus (Figure 1) and in hand area of the premotor cortex (area 6).

Overall, these observations support the idea that the posterior parietal cortex is an important focus in the highly distributed and interactive network of higher order cortical areas contributing to visuospatial analysis and to visuomotor commands. Different regions within the large inferior parietal lobule appear to be specialized for

different aspects of these higher neural computations, and these anatomical observations provide a structural basis for the existence of these distinctions.

Of tremendous interest is how the parietal lobule integrates the various sensory cues and translates them into motor commands, whether they be oculomotor saccades, smooth pursuit eye movements, or somatomotor hand action. A property common to many areas within the parietal lobe is the modulation of parietal neuronal discharge with attention (see chapter in this volume by Shimojo). Where do these signals arise? What is the precise contribution of the parietal cortex in the integration of visual and motor signals in smooth tracking movements (see chapter in this volume by Kawano). The vigorous pursuit of these and other important issues associated with visual and oculomotor functions will provide us with more insight into the integrative nature of the higher order neural functions subserved by the various cortical fields within the posterior parietal cortex.

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