

Further Observations on Parieto-Temporal Connections in the Rhesus Monkey*

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Summary. The origin, course, and termination of parieto-temporal connections in the rhesus monkey were studied by autoradiographic techniques. The caudal third of the inferior parietal lobule (including the adjacent lower bank of the intraparietal sulcus) is the chief source of these projections. It projects to three separate architectonic areas in the superior temporal sulcus and to three different areas on the ventral surface of the temporal lobe: the parahippocampal gyrus, presubiculum, and perirhinal cortex. The mid-inferior parietal lobule and medial surface of the parietal lobe, by contrast, project only to the caudal upper bank of the superior temporal sulcus. The rostral inferior parietal lobule and the superior parietal lobule, as well as the postcentral gyrus and rostral parietal operculum, do not project to the temporal lobe. Fibers travel from the posterior parietal region to temporal cortex by way of several different routes. One fiber bundle courses in the superior temporal gyrus and terminates in the superior temporal sulcus. Another proceeds ventrally, between the depth of the superior temporal sulcus and the geniculocalcarine tract, to the parahippocampal area. A separate bundle, coursing part of the way in the company of the cingulum bundle, conveys posterior parietal fibers to the presubiculum.

Key words: Parietal lobe – Temporal lobe – Cortical connections

Introduction

Several previous neuroanatomical studies have demonstrated cortical projections from the parietal to the temporal lobe in the rhesus monkey (Pandya and Kuypers 1969; Jones and Powell 1970; Seltzer and Pandya 1976, 1978; Seltzer and Van Hoesen 1980). Parieto-temporal connections originate in posterior parietal "association" cortex. They terminate in three architectonically distinct zones in the cortex of the superior temporal sulcus and in three different regions on the ventral surface of the temporal lobe: the parahippocampal area, presubiculum, and perirhinal cortex. These observations notwithstanding, a number of questions still persist with regard to parieto-temporal connections. For example, what is the precise source, within the parietal lobe, of projections to the temporal lobe? Although earlier studies pointed to the inferior parietal lobule as the major source of these pathways, the precise location of their origin was not determined. Nor was it shown whether projections to different regions of the temporal lobe emanate from the same, or different, parietal cortical zones. Moreover, in previous studies, possible temporal lobe projections of two large sectors of posterior parietal cortex, viz. the medial surface of the parietal lobe and the intraparietal sulcus, were not explored. Questions also persist with regard to the mode of termination of parieto-temporal connections. How are they distributed to the various architectonic divisions of the temporal lobe? What is their laminar pattern of termination? Finally, what route is taken by these fibers as they travel from the parietal to the temporal lobe? The present study attempts to answer these questions relating to parieto-temporal connections by means of the autoradiographic technique.

Materials and Methods

In nineteen rhesus monkeys, discrete injections of radiolabelled amino acids (³H-leucine and/or -proline; volume range, $0.4-1.0 \mu$ l; specific activity range, $40-80 \mu$ Ci/ μ l) were made into different

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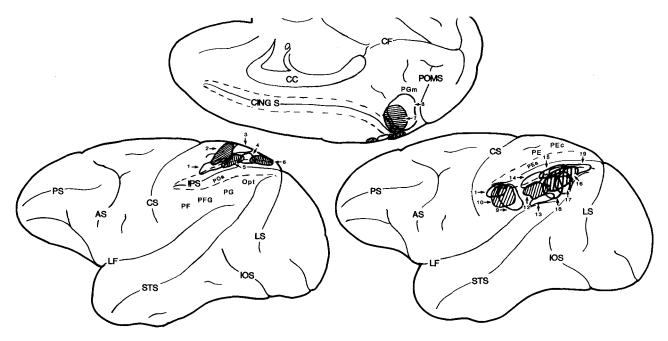


Fig. 1. Drawings of the lateral and medial surfaces of the cerebral hemisphere in the rhesus monkey to show the sites of isotope injections (1–19) and the architectonic parcellation of the posterior parietal lobe. Abbreviations in this and subsequent figures: AS, arcuate sulcus; CC, corpus callosum; CF, calcarine fissure; CINGS, cingulate sulcus; ILF, inferior longitudinal fasciculus; IOS, inferior occipital sulcus; IPS, intraparietal sulcus; LF, lateral (Sylvian) fissure; LS, lunate sulcus; MdLF, middle longitudinal fasciculus; MOS, medial orbital sulcus; OIS, occipito-inferior sulcus; OLF, olfactory tract; OTS, occipitotemporal sulcus; POMS, parieto-occipital medial sulcus; PRESUB, presubiculum; PS, principal sulcus; RhF, rhinal fissure; STS, superior temporal sulcus

sectors of posterior parietal cortex and, after seven to ten days' survival, the brains were processed for autoradiography (Cowan et al. 1972). Taken together, injections covered nearly the entire parietal lobe behind the postcentral gyrus, including the medial surface of the parietal lobe and the cortex of the intraparietal sulcus. Exposure times ranged from three to six months. Coronal sections of the ipsilateral hemisphere were then examined under dark-field light microscopy, and silver grains indicative of terminal labelling in the temporal lobe were charted. The same material was also used to trace the course of labelled fiber bundles from the injection sites, through the underlying white matter, to their terminations in the temporal lobe. In addition, a series of thioninstained sections was examined under bright-field light microscopy in order to locate, in terms of cortical cytoarchitecture, the site of each injection and its projection(s) within the temporal lobe. The architectonic nomenclature employed in this study derives from the parcellations of Bonin and Bailey (1947), Pandya and Seltzer (1982) (Fig. 1), Rosene and Pandya (1983) (Fig. 4), and Selzer and Pandya (1978) (Fig. 4).

Results

Superior Parietal Lobule, Upper Bank of the Intraparietal Sulcus, and Medial Surface of the Parietal Lobe (Areas PE, PEa, PEc, and PGm)

There were eight monkeys with injections of radiolabelled amino acids in these sectors of the

posterior parietal lobe (Fig. 1). Five (cases 1-5) had injections of the superior parietal lobule and/or upper bank of the intraparietal sulcus (areas PE and PEa). All of these cases failed to show evidence of terminal labelling in the temporal lobe. By contrast, the three other animals, with injections at the apex of the superior parietal lobule (area PEc; case 6) and on the medial surface of the parietal lobe (areas PEc and PGm; cases 7 and 8), did demonstrate a projection to temporal neocortex. As shown in Fig. 2 (case 8), labelled fibers emerged from the injection site and descended in the white matter between the medial surface of the parietal lobe and the upper bank of the intraparietal sulcus. Reaching the depth of the intraparietal sulcus, they then coursed laterally to distribute labelling over the upper bank of the superior temporal sulcus in its caudal segment. This was located principally within the confines of architectonic area TPO although, in cases 7 and 8, there was some additional terminal label in the adjacent sulcal sector, area PGa. Within the target zones, labelling was disposed in columnar fashion over all six layers of cortex with terminal label concentrated in and around layer IV. None of these cases showed any terminal label in ventral temporal cortical regions.

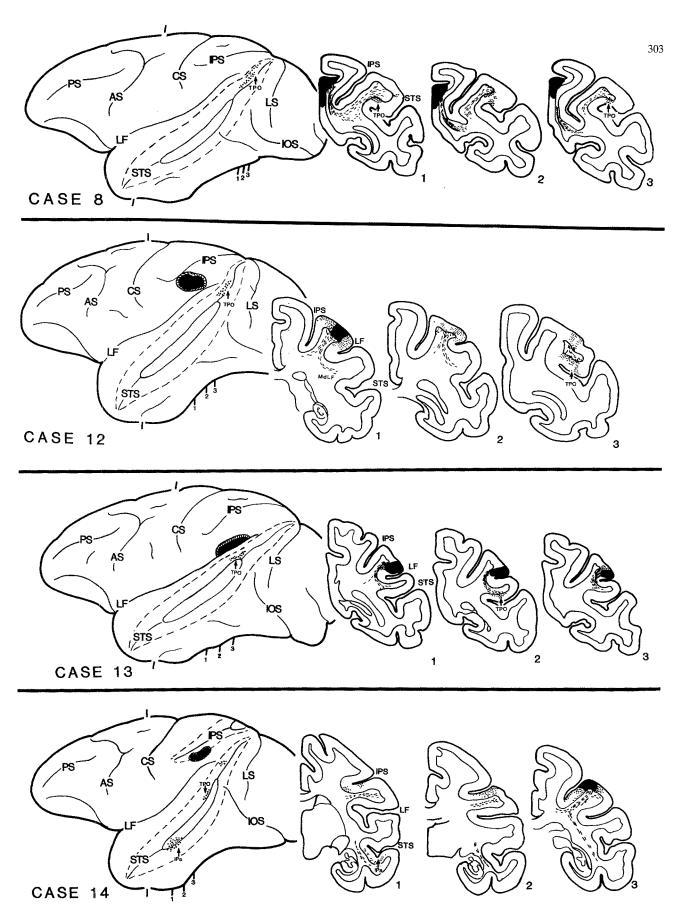


Fig. 2. Diagrammatic representation of the distribution of terminal label (shown as dots) within the temporal lobe of four cases with injections (drawn in black) of the medial surface of the parietal lobe and the mid-inferior parietal lobule. Labelled fiber bundles are shown as interrupted lines. Coronal sections are taken from the levels indicated on the lateral surface

Inferior Parietal Lobule, Parietal Operculum, and Lower Bank of the Intraparietal Sulcus (Areas PF, PFG, PFop, PG, PGop, and Opt)

There were eleven monkeys with injections in these cortical areas (Fig. 1). Only those with injections in the middle and caudal thirds of the inferior parietal lobule and/or adjacent lower bank of the intraparietal sulcus were found to have projections to the temporal lobe. Injections in the rostral third of the inferior parietal lobule (area PF and rostral area PFG; cases 9–11) were entirely devoid of terminal labelling in the temporal lobe.

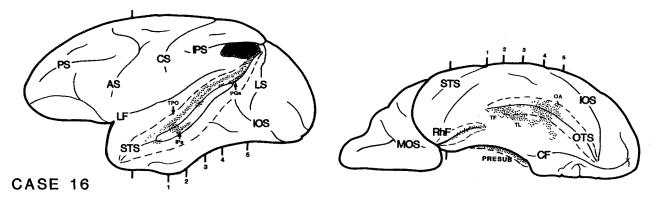
Three monkeys (cases 12-14) had injections in the mid-inferior parietal lobule (caudal area PFG and rostral area PG) (Fig. 2). In case 12 the injection was in the central portion of the mid-inferior parietal lobule while that of case 13 involved the ventral sector and extended into the upper bank of the lateral sulcus. In case 14, the injection was placed more dorsally and encroached upon the lower lip of the intraparietal sulcus. In each of these three cases labelled fibers emerged from the injection site and coursed ventromedially around the depth of the lateral sulcus before terminating over area TPO in the upper bank of the caudal portion of the superior temporal sulcus (Fig. 2). Case 14, however, had an additional focus of silver grains located more rostrally and ventrally, over cortex in the depth of the superior temporal sulcus. This target zone corresponded, in architectonic terms, to area IPa (Seltzer and Pandya 1978). A similar pattern of labelling in the superior temporal sulcus, i.e. over the caudal upper bank (area TPO) and rostral depth (area IPa), was also seen in one other experimental animal, case 15 (not illustrated). In this case, the injection involved the lower lip of the intraparietal sulcus slightly caudal to the injection site of case 14. The laminar pattern of termination in all of these cases was similar to that of case 8 (see above).

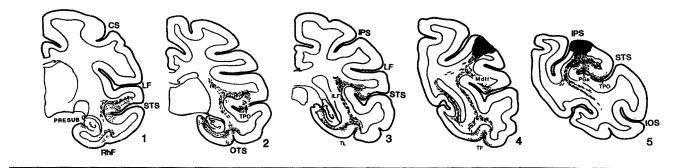
Unlike the cases described thus far, those with injections in the *caudal* third of the inferior parietal lobule and adjacent lower lip of the intraparietal sulcus (caudal area PG and area Opt; cases 16–19) had substantial projections to the cortex of the temporal lobe (Fig. 3). The injection site in case 16 extended from the lower lip of the intraparietal sulcus to the upper bank of the superior temporal sulcus. As shown in Fig. 3, this case displayed three distinct foci of terminal label in the superior temporal sulcus. In the upper bank, two parallel bands of silver grains were observed. These could be traced forward, more or less continuously, from the caudal limit of the sulcus to the level of the ventral tip of the central sulcus. The more laterally-placed band of

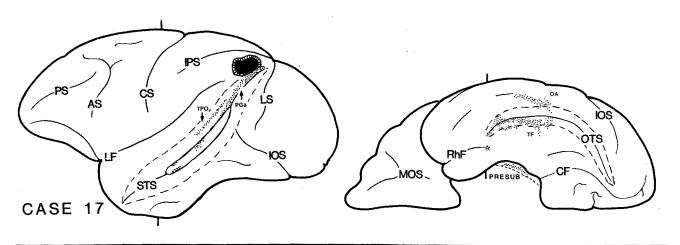
silver grains was situated over a small secondary gyrus in the upper bank of the superior temporal sulcus. This corresponded to area TPO. In this architectonic zone, terminal label was disposed in the form of columns running perpendicular to the pial surface and extending over all six layers of cortex. The infragranular layers (V and VI), however, showed predominantly labelled fibers whereas silver grains indicating terminals were concentrated in the supragranular layers (I to IV) (Fig. 6A). The second band of terminal label, which was somewhat more interrupted in the rostrocaudal dimension, was located medially, at the upper shoulder of the superior temporal sulcus. This corresponded to area PGa. It exhibited a similar laminar pattern of termination (Fig. 6A). A third, and final, focus of terminal label in the superior temporal sulcus was observed over cortex in the rostral portion of the depth of the sulcus, corresponding to area IPa. Here terminal label was also distributed in columnar fashion (Fig. 6B). Besides these three foci of terminal labelling in the superior temporal sulcus, a small focus of silver grains was observed over the caudalmost sector of the superior temporal gyrus (area Tpt; Pandya and Sanides 1973).

Case 16 also displayed evidence of projections to the ventral portion of the temporal lobe (Fig. 3). Two separate foci of terminal labelling occurred over the parahippocampal area. One was situated in the medial bank of the occipitotemporal sulcus over architectonic area TF. The other was situated more medially, over the adjacent parahippocampal area TL (Rosene and Pandya 1983). In both parahippocampal sectors label was organized in columnar fashion (Fig. 6C and D) with predominance of label in and around layer IV. In addition, terminal label was also seen over the presubiculum (area 27). In that area, silver grains appeared to be concentrated over the first and second layers and were present to the maximal extent at caudal levels (Fig. 6C and D). Another cluster of terminal label was encountered over both banks of the rhinal fissure in the perirhinal cortex (area 35a and b) (Fig. 3, Sect. 1). Finally, at caudal levels, silver grains were observed over occipito-temporal cortex (area OA) of the ventral peristriate belt. In this location, label was seen mainly over the first cortical cell layer. However, some grains were also observed in layers V and VI.

Two other experimental animals (cases 17 and 18) also had injections in the caudal third of the inferior parietal lobule (caudal area PG and area Opt), but these injections primarily involved the ventral sector and did not impinge upon the lower bank of the intraparietal sulcus. Overall, the pattern of terminal labelling in the temporal lobe was similar







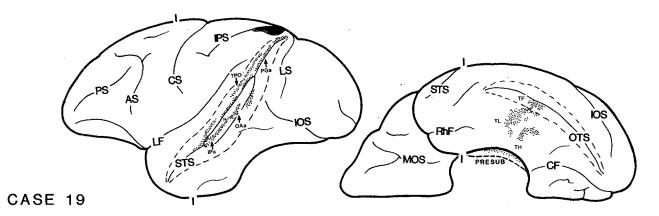


Fig. 3. Diagrammatic representation of the distribution of terminal label within the temporal lobe of three cases with injections of the caudal third of the inferior parietal lobule. Coronal sections in case 16 also show the course of labelled fibers leading to the temporal lobe

to that of case 16 (Fig. 3 illustrates case 17). Several differences, however, were noted. Labelling of the upper bank of the superior temporal sulcus (areas TPO and PGa) did not extend as far rostral as it did in case 16, and labelling of area IPa was scant. Furthermore, with regard to the ventral temporal lobe, labelling was largely restricted to area TF in the parahippocampal gyrus with area TL relatively free of silver grains (cf. case 16). There was a heavy concentration of silver grains over the presubiculum, but only minimal amounts over the perirhinal region.

In case 19, the injection of the caudal third of the inferior parietal lobule extended dorsally into the lower bank of the intraparietal sulcus where, at caudal levels, it involved a portion of area OA. This case resembled case 16 in that it displayed silver grains over both caudal and rostral portions of areas TPO and PGa as well as over area IPa in the superior temporal sulcus (Fig. 3). Unique to this case, however, was the presence of terminal label over area OAa (Seltzer and Pandya 1978) in the caudal depth and lower bank of that sulcus. Moreover, on the ventral surface, labelling of the parahippocampal gyrus was found over the medial architectonic sector, area TH, in addition to the intermediate and lateral areas TL and TF. A small amount of silver grain occurred over the presubiculum, but there was none over the perirhinal cortex and ventral persistriate belt (area OA).

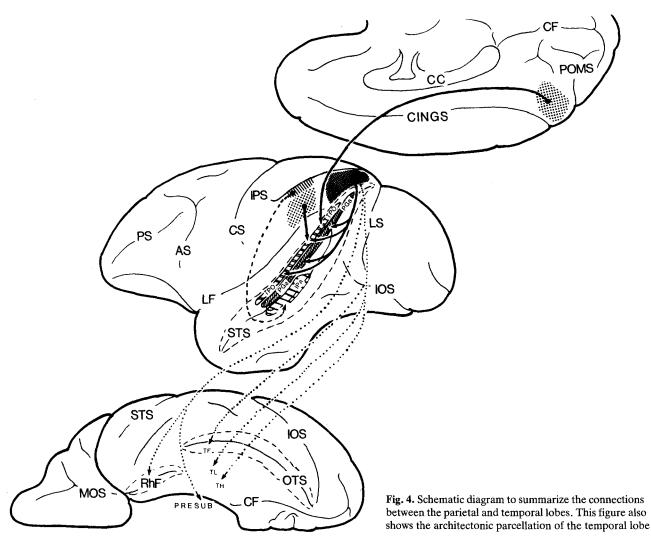
From injections in the caudal third of the inferior parietal lobule (caudal area PG and area Opt), three different fiber pathways were traced to their terminations in the temporal lobe. One prominent bundle of labelled fibers descended from the injection site into the white matter of the superior temporal gyrus. From this location, fibers entered the upper bank of the superior temporal sulcus along its caudal-torostral course and terminated in areas TPO, PGa, and IPa (Figs. 3, 6E–G). This fiber bundle is termed the "middle longitudinal fasciculus" (MdLF) (see Discussion).

Fibers travelling from the caudal inferior parietal lobule to the *ventral* surface of the temporal lobe took a different route. After emerging from the injection site, a distinct bundle of labelled fibers coursed ventrally into the temporal lobe, between the white matter underlying the depth of the superior temporal sulcus and the geniculocalcarine tract, as far as the occipitotemporal sulcus. Labelled fascicles then entered the cortex of the ventral temporal lobe, terminating in the parahippocampal gyrus (areas TF, TL, and TH) (Figs. 3, 6E–G) and the ventral peristriate belt (area OA). This fiber bundle corresponds to the inferior longitudinal fasciculus ("ILF") of Dejerine (1895) (see Discussion). A separate fiber bundle led from the caudal inferior parietal lobule to the presubiculum. This fascicle coursed medially around the splenium of the corpus callosum to enter the white matter of the calcarine fissure (Fig. 3, case 16; Fig. 6E and F). At this point it joined the fibers of the ventral cingulum bundle and terminated in the presubiculum (Fig. 6G).

Discussion

The present study confirms and extends previous observations on parieto-temporal connections in the rhesus monkey (Fig. 4). The source of these projections is limited. A discrete region in the caudal third of the inferior parietal lobule, corresponding to the caudal portion of area PG and area Opt (Pandya and Seltzer 1982), gives rise to the majority of parietotemporal projections. It is the chief source of parietal projections to the superior temporal sulcus and the only source of projections to the ventral temporal region (parahippocampal area, presubiculum, and perirhinal cortex). Although other posterior parietal regions, viz. the mid-inferior parietal lobule (caudal area PFG and rostral area PG) and medial parietal cortex (areas PEc and PGm), also connect with the temporal lobe, they send only modest projections to the superior temporal sulcus and none to the ventral temporal region.

The cortex of the superior temporal sulcus is a major target of parieto-temporal connections. Two adjacent, elongated architectonic sectors in its upper bank, designated as areas TPO and PGa in a previous study (Seltzer and Pandya 1978), receive extensive projections from the caudal third of the inferior parietal lobule (caudal area PG and area Opt) along their rostrocaudal extent. They also receive, in their caudal segments, projections from the mid-inferior parietal lobule (caudal area PFG and rostral area PG) and the cortex on the medial surface of the parietal lobe (areas PEc and PGm). Another architectonic sector located in the depth of the superior temporal sulcus, area IPa, is also a recipient of posterior parietal projections. Since injections encroaching upon the lower lip of the intraparietal sulcus consistently produce terminal labelling in this area while those in the ventral sector of the caudal inferior parietal lobule (e.g. case 17) do not, the projection to area IPa appears to derive from the dorsal portion of the caudal inferior parietal lobule along the lower lip of the intraparietal sulcus.



The ventral temporal region is the other major recipient of parieto-temporal connections. These derive exclusively from the caudal third of the inferior parietal lobule (caudal area PG and area Opt). The presubiculum and perirhinal cortex receive projections from the central portion of the caudal inferior parietal lobule. The projection to the parahippocampal gyrus, however, appears to have a topographical organization. This is because injections in the ventral sector of the caudal inferior parietal lobule produce terminal label predominantly in the lateral portion of the parahippocampal gyrus, area TF (e.g. case 17), while dorsal injections, encroaching upon the lower bank of the intraparietal sulcus, also label the medial parahippocampal gyrus, area TH (e.g. case 19). The intermediate parahippocampal zone, area TL (Rosene and Pandya 1983), appears to receive projections from the central portion of the caudal inferior parietal lobule. Injections

restricted to the ventral portion of the caudal inferior parietal lobule also produce label in the first cell layer of occipitotemporal cortex (area OA) in the ventral peristriate belt. This may be attributed to the injection of isotope into area Opt, since area Opt has been shown previously (Pandya and Seltzer 1982) to project to the first layer of cortex of the peristriate belt (area OA). By contrast, injections of the dorsal portion of the caudal inferior parietal lobule, which involve OA-type cortex in the lower bank of the caudal intraparietal sulcus (e.g. case 19), project to a distinct architectonic sector, area OAa (corresponding to area "MT"; Van Essen et al. 1981), in the depth and lower bank of the superior temporal sulcus. In this respect, they resemble injections of area OA reported in other studies of cortical connections (Montero 1980; Rockland and Pandya 1979; Seltzer and Pandya 1978; Ungerleider and Mishkin 1979; Zeki 1976).

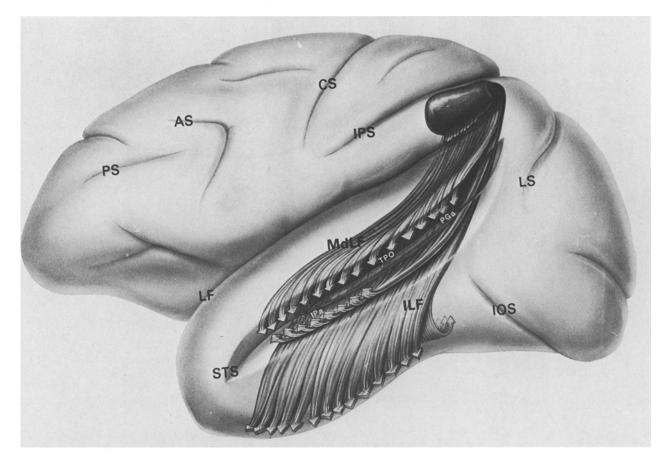


Fig. 5. Artist's rendering of the course of two major fiber bundle pathways connecting the caudal inferior parietal lobule with the temporal lobe. The middle longitudinal fasciculus (MdLF) leads to the superior temporal sulcus and the inferior longitudinal fasciculus (ILF) to the ventral surface of the temporal lobe

The fiber pathways connecting the parietal with the temporal lobe are organized in discrete bundles. From the caudal third of the inferior parietal lobule (caudal area PG and area Opt), three distinct long association fiber bundles travel to the temporal lobe. One proceeds rostroventrally in the core of the superior temporal gyrus and leads to terminations in the upper bank and depth of the superior temporal sulcus (areas TPO, PGa, and IPa) (Fig. 5, "MdLF"). Another bundle courses ventrally, between the white matter subjacent to the superior temporal sulcus and the optic radiation, to the ventral surface of the temporal lobe where it conveys fibers to the parahippocampal gyrus (areas TF, TH, and TL) and the ventral peristriate belt (area OA) (Fig. 5, "ILF"). The third bundle emerges from the caudal inferior parietal lobule and travels medially, arching around the splenium of the corpus callosum, to join the fibers of the cingulum bundle and terminate in the presubiculum.

In describing the white matter fiber bundles of

the human brain, Dejerine (1895) designated as the "superior longitudinal fasciculus" a prominent bundle that courses longitudinally in the cerebral hemisphere just above the level of the Sylvian fissure. According to Dejerine, the superior longitudinal fasciculus conveys fibers in a rostral direction to the frontal lobe from the occipital and parietal lobes as well as from the caudal portion of the superior temporal region. This latter component has been termed the "arcuate fasciculus". The white matter bundle in the superior temporal gyrus identified in the present study, by contrast, conveys fibers from the posterior parietal lobe to the superior temporal sulcus. It, therefore, appears to be distinct from the superior longitudinal fasciculus, and we have termed it the "middle longitudinal fasciculus".

The parietal fibers which lead to the ventral surface of the temporal lobe appear to course within what Dejerine (1895) termed the "inferior longitudinal fasciculus." According to Dejerine, however, fibers of the inferior longitudinal fasciculus originate

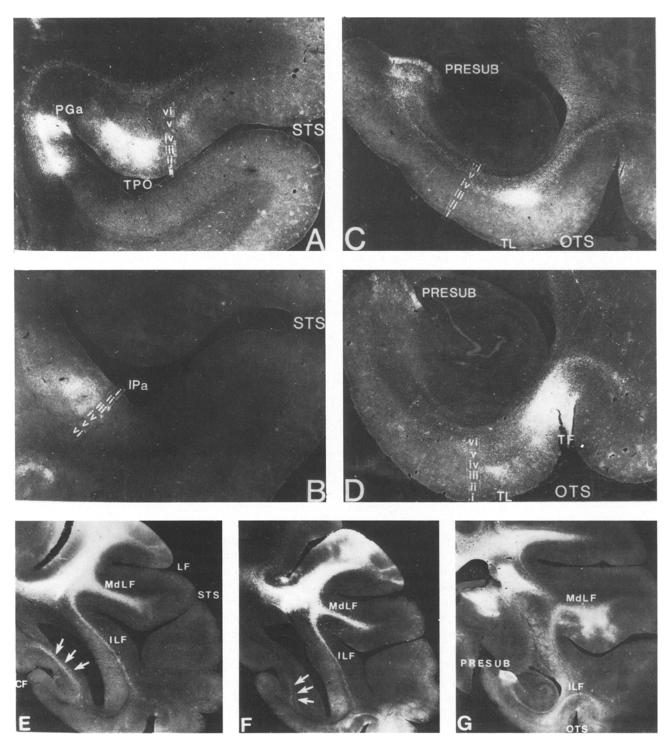


Fig. 6A–G. Photomicrographs of coronal sections of the hemisphere A–D show the laminar distribution (layers i-vi) of silver grains in various architectonic divisions of the superior temporal sulcus (A and B) and ventral temporal lobe (C and D) after an injection in the caudal inferior parietal lobule (case 16) (sections A and C are caudal to sections B and D). E–G show the course of labelled fibers in the temporal lobe following the same injection. Note the middle longitudinal fasciculus (MdLF) and the inferior longitudinal fasciculus (ILF). Arrows indicate a separate bundle of labelled fibers leading to the presubiculum. $\times 4$

in the occipital and temporal lobes while the present study demonstrates a substantial contribution to this bundle from the posterior parietal lobe. Moreover, Dejerine described another component of the inferior longitudinal fasciculus which courses around the splenium of the corpus callosum and leads to the hippocampus. In the present study, a similar fiber bundle following an identical route was also observed, but it was found to originate in posterior parietal cortex and to terminate in the presubiculum. It is interesting to note, however, that for part of their course, these fibers accompany the ventral component of the cingulum bundle, a fiber pathway which also leads to the presubiculum (Mufson and Pandya, in press).

In an effort to understand the functional significances of the parieto-temporal connections reported in this study, it may be useful to consider first the nature of their sources in posterior parietal association cortex. In a recent study of the architectonics and intrinsic connections of posterior parietal cortex (Pandya and Seltzer 1982), a fundamental distinction was found to exist between the superior parietal lobule (areas PE, PEa and PEc), medial parietal cortex (area PGm), and rostral and mid-inferior parietal lobule (including the lower rim of the intraparietal sulcus) (areas PF, PFG and rostral area PG), on the one hand, and the caudal third of the inferior parietal lobule (caudal area PG and area Opt), on the other. The former areas receive relatively direct, topographically-organized somatic sensory cortical input and may, therefore, be presumed to subserve somatic sensory-related functions. Numerous physiological and behavioral studies confirm this putative role (Duffy and Burchfiel 1971; Moffett et al. 1967; Sakata et al. 1973). The latter area, i.e. caudal inferior parietal lobule, by contrast, receives topographically-convergent somatic sensory input as well as visual-related afferents. This pattern of connections suggests a more complex, non-modality-specific, integrative function. Both physiological and behavioral studies of the inferior parietal lobule (Hyvärinen 1981; Mountcastle et al. 1975; Robinson et al. 1978) support this prediction.

Put in this context, parieto-temporal connections may be conceptualized as being of two types. One type consists of those projections emanating from the modality-specific zones, e.g. mid-inferior parietal lobule, lower lip of the intraparietal sulcus, and cortex on the medial surface of the parietal lobe. These projections, which are relatively sparse and are directed to the caudal segments of areas TPO and PGa and to area IPa in the superior temporal sulcus, may be conveying somatic sensory information to the temporal lobe. For example, the projection to area IPa from the lower lip of the intraparietal sulcus may be carrying somatic sensory information relating to the contralateral face, head, and neck since this sequence of connections may be traced back to the ventral part of the postcentral gyrus (area 2). The second category of parieto-temporal connections comprises those projections originating in the caudal inferior parietal lobule. Much more substantial than those described above, these afferents terminate throughout areas TPO and PGa in the superior temporal sulcus as well as in the parahippocampal gyrus, presubiculum, and perirhinal cortex of the ventral temporal lobe. Because of the nature of the cortical zone from which they originate, these projections might be presumed to convey highly complex, non-modality-specific information, possibly visuospatial in nature (Ungerleider and Mishkin 1982).

In previous anatomical studies (Jones and Powell 1970; Seltzer and Pandya 1978), the superior temporal sulcus has been shown to receive cortical input from auditory and visual association cortices as well as from the posterior parietal lobe. The different sensory-related inputs are organized in a complex pattern of overlapping and nonoverlapping zones. The present study traces presumptive somatic sensory cortical input to certain limited sectors of the sulcus, viz. caudal segments of areas TPO and PGa and area IPa. It is apparent, however, that the preponderance of parietal projections to the superior temporal sulcus do not originate in unimodal somatic sensory association cortex but rather in the connectionally-complex caudal inferior parietal lobule. Although the precise functional significance of these parietal lobe projections to the superior temporal sulcus is not clear, the pattern of projections suggests that they are concerned, at least in part, with the further elaboration and cross-modal integration of both somatic sensory and visuospatial information.

The parahippocampal area in another cortical region which receives auditory- and visual-related cortical input in addition to afferents from posterior parietal cortex (Jones and Powell 1970; Seltzer and Pandya 1976). As in the superior temporal sulcus, the different sensory-related afferents in the parahippocampal gyrus are arranged in overlapping and nonoverlapping zones. According to the present study, parietal input to the parahippocampal gyrus derives exclusively from the caudal inferior parietal lobule. This suggests that it is not simple somatic sensory information, but highly processed somatic sensory data already integrated with visual information, that enters the parahippocampal gyrus by this route. Since the parahippocampal gyrus projects to the entorhinal region which, in turn, connects with the hippocampus (Van Hoesen et al. 1972; Van

Hoesen 1982), the projection of the caudal inferior parietal lobule to the parahippocampal area may be viewed as one link in a chain of pathways connecting complex sensory association cortex with the limbic system. Similarly, the projections of the caudal inferior parietal lobule to the presubiculum and perirhinal region, both of which also connect with the hippocampus (Shipley 1975; Van Hoesen 1982; Van Hoesen and Pandya 1975), may also be routes of access of complex sensory information to the limbic system. The differential functional significance of the three parallel posterior parietal-to-limbic, viz. parahippocampal, presubicular, perirhinal, connectional sequences is not immediately apparent. The sequence leading through the parahippocampal gyrus, however, is an indirect pathway to the limbic system. Moreover, because the parahippocampal gyrus has other sensory-related cortical inputs (Jones and Powell 1970; Seltzer and Pandya 1976), visuosomatic sensory input travelling this route might interact further with other visual, as well as auditory, data before entering the limbic system. The parietalpresubicular and parietal-perirhinal pathways, on the other hand, bypass further sensory interactions and provide a more direct route to the limbic system. Since the caudal inferior parietal lobule is believed to play an important role in the mechanism of directed attention (Mesulam 1981), these particular parietolimbic connections may be involved in rapidly alerting the organism to motivationally significant stimuli in the environment.

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