CONNECTIONS OF THE PARietAL LOBE

J. M. PETRAS

Department of Neurophysiology, Division of Neuropsychiatry, Walter Reed Army Institute of Research, Washington, D.C. 20012

INTRODUCTION

The parietal lobes of the brains of primates exhibit an increase in fissuration and gyral complexity when comparing prosimians with New World and Old World monkeys, and some species of ceboids and cercopithecids with the apes and man. Increases in fissuration and gyration can be seen among the New World species themselves. Ample attention has been given to the great increase in size of the frontal lobes among primates, but a similar importance clearly should be attached to the parietal lobes of primates, and most probably to the temporal lobes as well. Our findings with respect to the anatomy of the parietal lobe suggest that the posterior part of the parietal lobe, i.e. the expanse of parietal cortex adjoining the somatic sensory region on the caudal side, undergoes an equally rapid development in several primate lines, such as ceboids and anthropoids, and that this development may indeed proceed somewhat in concert with the growth of the frontal lobes. The present account will serve to report and discuss evidence that the parietal lobe is connected with (i) the granular frontal cortex, directly as well as via a transcortical and transthalamic circuit with the temporal cortex, and (ii) the limbic system, more especially the cingulate gyrus, by direct associations and also more indirectly by way of a transthalamic pathway involving the nucleus lateralis dorsalis thalami.

Severe agnosias, apraxias and aphasias may beset man following infarction of the parietal lobes. Cerebrovascular accidents and cerebral tumors commonly cause tissue destruction extensive enough to involve both parietal lobules as well as adjoining regions of the occipital or temporal isocortex. Clinico-pathological studies have led to the identification of polyesthesias, hallucinations, graphesthesias, ahylognoses, amorphognosia and constructional apraxia as symptoms attributable to parietal lobe involvement. Dyscalculia, dysgraphia, finger-agnosia, right and left-sided disorientation (Gerstmann's syndrome) have been found symptomatic of lesions involving the supramarginal and angular gyri of the inferior parietal lobule together with adjacent occipital gyri, with or without additional involvement of the adjoining superior temporal convolution. In such cases, visual agnosias and disorientation are also commonly present. Disorders of body-image such as lack of awareness or complete denial of one-half of the body may be caused by lesions of the posterior parietal cortex and adjacent cortical territories. In experimental studies in the rhesus monkey and chimpanzee tactile agnosias such as barognosis, amorphogenesis and ahylognosis have been found to follow ablations of the posterior parietal cortex. It thus
appears that in such anthropoids as well as in man, the integrity of the parietal association cortex is required if tactile and proprioceptive signals are to gain emotional color and qualitative value.

Disconnection of the parietal lobes severely impairs the association of the somatic sensorium with visual, auditory, or olfactory informations obtained from the environment. The anatomical basis of such cortical syndromes requires elaborate study, a time-consuming and tedious process because of the enormous amount of labor involved in the tracing of widely distributed fiber connections by the use of fiber degeneration techniques. The present report represents but a brief beginning of this task.

**MATERIALS AND METHODS**

This report is based on findings made in ten rhesus monkeys (Macaca mulatta) in which various parts of the superior (areas 5 and 7 of Brodmann) and inferior (area 7 of Brodmann) parietal lobules had been removed by aspiration of cortical gray matter. All operations were performed under aseptic conditions in animals deeply anesthetized with Nembutal, and every precaution was taken to minimize damage to the subjacent white matter. The superior lobules were lesioned unilaterally in three monkeys, and bilaterally in one animal. Five monkeys sustained lesions of the inferior lobule; in one monkey the inferior lobule was lesioned on both sides. Area 5 of the left hemisphere and area 7 of the right hemisphere were lesioned in one other monkey.

The animals were allowed to survive from 12 to 18 days, except for one animal which received bilateral lesions of the inferior parietal lobule (area 7) on separate days and was subsequently sacrificed to provide survival times of 13 and 4 days after surgery. All animals were killed in deep anesthesia by exsanguination and transcardial perfusion with physiological saline followed by 10 per cent formalin for fixation. The brains and spinal cords were removed immediately after the perfusion, and further fixed in 10 per cent formalin.* Serial transverse sections of the brain were cut on the freezing microtome at 26μ and 52μ, and collected in 10 per cent formalin. Serial sections were stained for degenerated fibers using the Nauta uranyl nitrate modification of the Nauta-Gygax* techniques, and the Fink-Heimer* methods. In some instances the Albrecht-Fernstrom* phosphotungstic acid modification of the Nauta-Gygax* method was used. Alternate sets of adjacent serial sections were stained for cell bodies with cresylechtviolet, and for myelinated fibers with the Weil method. These supplementary series provided an important aid in determining the cytoarchitectonic and myeloarchitectonic identity of the structures shown by the silver methods to contain degenerating nerve fibers. Additional material available for the study of the normal anatomy of the cortex and subcortical nuclei included brains cut frozen at 200μ thickness or after celloidin embedding cut at 36μ thickness.

The distribution of degenerated fibers of passage and the location of terminal degeneration in the cortex and subcortical nuclei were determined microscopically and recorded in projection drawings of the actual sections.

* This study was performed in strict adherence to the Guide for Laboratory Animal Facilities and Care, published by the Institute of Laboratory Animal Resources, National Academy of Sciences-National Research Council.
RESULTS AND DISCUSSION

This report can be considered a somewhat preliminary documentation of current studies concerning the efferent connections of the parietal lobules of the rhesus monkey. The material available is still being analyzed, and only the clearest evidence of parietal lobe connections with other cortical regions and with the basal ganglia, the thalamus and the midbrain will here be reported and discussed.

The superior parietal lobule

A large bundle of degenerated fibers leaves the superior parietal lobule and traverses the centrum semiovale before entering the internal capsule. Some of these fibers leave the superior lobule in a nearly vertical direction to enter the extreme and external capsules which they follow as routes to their distribution fields in the claustrum and putamen. Additional degenerating fibers coursing through the extreme capsule enter the dorsal portion of the insular cortex which contains numerous degenerating axon ramifications, especially abundant in the infragranular layers. A field of very dense terminal degeneration occupies the dorsal two-thirds, and tapers to a narrow lateral zone in a more ventral part of the putamen. Terminal degeneration is also present in the body of the caudate nucleus, but no degenerating fibers can be identified in the globus pallidus.

Dense terminal degeneration is present in the nucleus lateralis posterior (LP) of the thalamus (Fig. 6) and extends among the adjacent cells of the nucleus reticularis thalami (R). The degenerated fibers enter the nucleus lateralis posterior from the internal capsule as components of the lateral thalamic peduncle by recurving in a medial and dorsal direction. The fibers are interspersed with medium-sized lightly stained neurons which are easily distinguished from the larger cells of the nucleus ventralis lateralis pars postrema (VLps), a cell group receiving cerebellothalamic fibers and fibers originating in the precentral (motor) gyrus. Ventral to the nucleus lateralis posterior is the nucleus ventralis posterior lateralis (VPL), composed of a mixed population of neurons, some of which are large and deeply chromatophilic, while others are smaller and of lighter color. The mixing of the dark cells with medium-sized lighter cells distinguishes VPL conspicuously from the nucleus lateralis posterior which has a somewhat denser population of more evenly spaced medium-sized round cells lacking an admixture of large cells (Fig. 9). The cytoarchitectonic differences between VLps, LP and VPL coincide well with the myeloarchitectonic structure of the same nuclei (compare Figs. 9–11). In myelin-stained sections LP is characterized by being extremely lightly stained (Fig. 11); in contrast with VLps and VPL it contains only sporadic bundles of heavily myelinated fibers. The fiber plexus of VLps appears much darker in myelin stains. The nucleus ventralis posterior lateralis (VPL) is richly populated with myelinated bundles oriented in nearly horizontal planes, but the nucleus is also penetrated by numerous dorsoventrally oriented myelinated fibers entering through its ventral border. Some of these fibers are components of the medial lemniscus, while others are cerebellofugal fibers destined for VLps and VLC (Fig. 14). The correspondence between the cytoarchitectonic and myeloarchitectonic appearance of these cell groups and the pattern of fiber degeneration in LP following superior parietal lobule lesions is remarkable.
FIG. 6. Fiber degeneration following ablation of the superior parietal lobule (area 5) in the rhesus monkey as described in the text. Degenerating fibers are indicated as thin, broken lines.
Numerous degenerating axons descend from the lesion in the superior parietal lobule through the internal capsule into the cerebral peduncle. At rostral levels of the subthalamic region such fibers can be seen to terminate in moderate numbers in the zona incerta and field H2 of Forel, but no degenerated terminal fibers can be identified in the subthalamic nucleus.

A more massive termination of this brainstem projection is evident in the pretectal area, superior colliculus, and pontine nuclei, but no degenerated terminal fibers can be identified in the substantia nigra. Terminal degeneration is dense in the pretectal region just medial or medioventral to the nucleus limitans of Olszewski, and also surrounds the region pretectalis anterior of Olszewski (nucleus olivarius of Kuhlenbeck and Miller). Dense terminal degeneration occupies an approximately vertical field at the transition between the superior colliculus and pretectal area. In the absence of an adequate cytoarchitectonic study, it is not clear to what extent the cellular organization of the simian pretectal region corresponds to the description of the region in the rat. In the latter species, Bucher and Nauta outlined three major cell groups, viz., nucleus pretectalis, nucleus pretectalis medialis and nucleus pretectalis profundus. In the present cases of lesion of the superior parietal lobule (area 5), a very dense terminal degeneration appeared in the ventrolateral part of the pretectal area bounded by the nucleus limitans and the nucleus suprageniculatus laterally, the mesencephalic reticular formation ventrally, and the superior colliculus and nucleus of the posterior commissure medially. It seems possible that this area corresponds to the nucleus pretectalis profundus of the rat.

The corticocortical connections of the superior lobule have not been fully mapped. It can nevertheless be demonstrated that lesions of the superior parietal lobule elicit degeneration of fibers extending to the contralateral superior and inferior parietal lobules, the ipsilateral premotor cortex, precentral and postcentral gyri, arcuate cortex, granular frontal cortex along the dorsal and ventral banks of the principal sulcus, cingulate gyrus (areas 23 and 24), inferior parietal lobule, insular cortex and superior temporal gyrus. The parieto-cingulate projection (to area 23 of Brodmann; LC of von Bonin and Bailey) is substantial. Pandya and Kuypers traced ipsilateral fibers of the superior lobule to the same areas: arcuate cortex, granular frontal cortex along the dorsal and ventral banks of the principal sulcus, premotor and motor cortex, postcentral gyrus, inferior parietal lobule, superior temporal gyrus, cingulate gyrus, and additional fibers to the preoccipital gyrus.

The inferior parietal lobule

Fiber degeneration can be traced from lesions of the inferior parietal lobule through the centrum semiovale of the cerebral hemisphere and into the internal capsule and cerebral peduncle. At the base of the lobule, degenerating fibers enter the dorsal parts of the insular cortex, forming a dense terminal plexus in the deep cortical cell layers IV–VI. The claustrum is invaded by degenerating fibers from its lateral and medial sides, the putamen by way of both the external and internal capsule. The dorsal two-thirds of the putamen contains a dense terminal degeneration. The body of the caudate nucleus is infiltrated by degenerated fibers which appear to terminate in greatest number in its lateral parts. No evidence of direct parietal projections to the globus pallidus was found in any of the cases studied.
FIG. 7. Axon degeneration following ablation of the inferior parietal lobule (area 7) of the rhesus monkey, as described in the text. Note dense terminal degeneration in the nucleus lateralis posterior of the thalamus immediately ventral to the nucleus lateralis dorsalis. Abundant terminal degeneration is also present in the nucleus lateralis dorsalis.
The parietothalamic fibers from the inferior lobule enter the thalamus from the internal capsule by curving under the caudate nucleus, and subsequently sweep over the nuclei VLps and VLc before entering the capsule of the nucleus lateralis dorsalis (LD) and terminating in that cell group. Other degenerated fibers pass directly through VLps and subsequently curve ventralward by bending inward from the capsule of the nucleus lateralis dorsalis prior to entering the nucleus lateralis posterior. The terminal distribution of fibers from the inferior parietal lobule appears to be confined to the dorsomedial cells of the nucleus lateralis posterior (Fig. 7). The corresponding projection from the superior lobule, by contrast, appears to affect preferentially the ventrolateral part of the nucleus.\textsuperscript{22}

In the ventral thalamus moderate fiber degeneration is seen in the zona incerta and field H\textsubscript{2} of Forel, but no evidence was found for the presence of terminal fibers in the subthalamic nucleus.

The corticocortical efferents of the inferior lobule have not been fully analyzed in these experiments, but connections with the contralateral superior and inferior lobules are evident, as are fibers to the ipsilateral prefrontal cortex, precentral and postcentral gyri, and a substantial connection with the adjacent cingulate gyrus (area 23). Another prominent bundle was traced via the external capsule toward the ventral surface of the temporal lobe. This fiber system distributes axons to the superior, middle and inferior temporal gyri, and to the fusiform gyrus. A portion of the projection reaching into the cranial part of the inferior temporal gyrus extends beyond this gyrus, following a medial direction and passing the shallow rhinal sulcus to terminate in the parahippocampal gyrus. Fiber degeneration in this gyrus is restricted to a sector of isocortex situated immediately lateral to the hippocampal formation and identified as TH by \textsc{von Bonin} and \textsc{Bailey}.\textsuperscript{20} Our preliminary data on intra- and interhemispheric connections, as also the fuller documentations of \textsc{Pandya} and \textsc{Kuypers},\textsuperscript{21} and \textsc{Pandya} and \textsc{Vignolo},\textsuperscript{23} suggest significant differences in the cortical associations of each of the parietal lobules. The projections from the inferior lobule involve particular regions of each of the gyri of the temporal lobe: superior, middle, and inferior temporal gyri, fusiform gyrus, and area TH of the parahippocampal gyrus. The superior parietal lobule, by contrast, entertains more limited connections with the temporal lobe that involve part of the ipsilateral superior temporal gyrus, and a small sector about midway rostrocaudally in the ventral bank of the contralateral superior temporal gyrus.\textsuperscript{23}

The inferior parietal lobule gives rise to still another prominent ipsilateral corticocortical fiber bundle. This substantial fiber group runs cranially in the hemisphere and distributes itself in a zone of the granular frontal cortex along the ventral bank of the principal sulcus.

\textsc{Pandya} and \textsc{Kuypers}\textsuperscript{21} reported evidence of similar ipsilateral corticocortical connections originating in the inferior lobule. They describe fibers to the superior parietal lobule, to a small cortical area in the caudal part of the superior temporal sulcus, the middle temporal gyrus, the postcentral and precentral gyri, the premotor and arcuate cortices, and to the granular frontal cortex ventral to the principal sulcus. Efferent connections to the contralateral insular cortex, cingulate gyrus, retrosplenial area, cortex along the occipitotemporal sulcus, and parahippocampal gyrus are also reported by \textsc{Pandya} and \textsc{Vignolo}.\textsuperscript{23}
Fig. 8. Parietofugal fibers were traced to the pretectal area and superior colliculus following superior and inferior parietal lobule lesions. These chartings illustrate some of the projections of the inferior lobule (area 7) to the pretectal area, to the central gray substance of the mesencephalon, and to the nuclei pontis Varolii.
The possibility of functional associations of the inferior parietal lobule with the limbic system can be clearly appreciated from the present experiments. The lobule has efferent connections not only with the cingulate gyrus but also with the nucleus lateralis dorsalis and with the temporal isocortex. In the monkey, Valenstein and Nauta have identified fibers to the nucleus lateralis dorsalis that appear to originate in either the septal region or hippocampus, or both. Projections of the inferior temporal gyrus have been traced by Whitlock and Nauta to the periamygdaloid part of the pyriform cortex, entorhinal area, amygdaloid complex (central, lateral, basal, and accessory basal nuclei), substantia innominata and, via the inferior thalamic peduncle, to the magnocellular part of the nucleus medialis dorsalis (MDmc of Olszewski). The parieto-temporal connection thus appears to be associated with the granular frontal cortex by way of two pathways from the temporal lobe to the mediodorsal nucleus. One of these temporo-thalamic connections is reciprocated by fibers that originate in the cortex of the frontal convexity and follow the uncinate fasciculus to the superior and middle temporal gyri and to a lesser extent to the inferior temporal cortex. The orbitofrontal cortex is reciprocally connected with the nucleus medialis dorsalis by a fiber system of rather precise topographic organization, and some degree of connective reciprocity also appears to exist between the amygdaloid complex and the nucleus medialis dorsalis of the thalamus. Numerous conduction routes are available, therefore, for the spread of somatic sensory information to the frontal granular cortex. Two of these routes are direct pathways and include fibers from the superior parietal lobule as well as a more massive projection from the inferior parietal lobule. Several further potential parieto-frontal conduction pathways involve the temporal lobe cortex, the temporo-thalamic and temporo-amygda-thalamic pathways, and the uncinate fasciculus.

Projections from the inferior parietal lobule to the mesencephalon are distributed to the pretectal area, the deeper layers of the superior colliculus, certain districts of the gray matter of the pons Varolii (Fig. 8), and the lateral densocellular central gray substance; but no evidence of a parieto-nigral projection was found in the present study. Parieto-pretectal and parieto-collicular fibers originating in both parietal lobules appear to involve to some extent at least the same general territories that are also projected upon by the retina, the cortical eye fields of the frontal lobe and the middle temporal gyrus. Kuypers and Lawrence found evidence of corticomesencephalic fibers to the superior colliculus originating in the premotor (area 6), arcuate (area 8), occipital and temporal cortices of the rhesus monkey. Such parietomesencephalic fibers could be thought to permit a direct dissemination of tactile and proprioceptive information to mesencephalic components of the visual system capable of integrating this information into mechanisms of visually guided behavior.

The multitude of cortical associations of the parietal lobules and their numerous subcortical connections makes it difficult to identify any one of them as the obvious explanation for parietal lobe syndromes. Some attention should be given, nevertheless, to the possible significance of parietal lobe connections with the cingulate gyrus, frontal granular
FIGS. 12, 13 and 14. Partial illustration of fiber degeneration in the thalamus following lesions of, respectively, the precentral gyrus\textsuperscript{16} (Fig. 12), the postcentral gyrus\textsuperscript{16} (Fig. 13) and the deep cerebellar nuclei\textsuperscript{4} (Fig. 14). Compare with present findings concerning parieto-thalamic projections shown in figs. 6 and 7, and note the striking correspondence between intrathalamic degeneration patterns on the one hand, and cyto- and myeloarchitectural delineations on the other. The VL\textsubscript{P} is a recipient of numerous fibers from the motor cortex and cerebellum, while LP receives fibers from the parietal lobules, but fails to receive afferent connections from the precentral and postcentral gyri or the cerebellum. The VPL receives afferent connections from the postcentral gyrus but appears not to be a recipient of fibers from the motor cortex or the cerebellum. A massive cerebellothalamic connection is established with the nucleus centralis lateralis and the ventromedial part of VL\textsubscript{C} (Fig. 14). Cerebellothalamic fiber connections are summarized and discussed further by MEHLER\textsuperscript{31} \textit{et. al.}, MEHLER\textsuperscript{32} and MEHLER\textsuperscript{33}.
cortex, and temporal isocortex. The efferent connections of the postcentral gyrus are more limited than those of the parietal lobules. The former projects to the posterior parietal lobules, precentral gyrus, premotor, arcuate, insular and cingulate cortices, but appears not to establish connections with the occipital or temporal lobes. The parietal lobules, in contrast, project to a rostral sector of the occipital lobe, and to wide areas of the frontal and temporal lobes, thus disseminating their neural codes to all other lobes of the cerebral cortex. The direct parietofrontal connections appear to be augmented by additional, and more indirect parietofrontal pathways which utilize the temporal isocortex and thalamus to reach lateral and orbital areas of the frontal granular cortex.

The results of Ruch et al. show that somatic sensory deficits may or may not follow parietal lobe lesions, depending upon the size of the lesion, the species involved, and the specific modality under consideration. Current evidence from animal experiments—chiefly in rhesus and mangabey monkeys—is inadequate to permit any definitive conclusion with respect to this comparative-neurological problem. Unfortunately, data from the human clinic are likewise often incomplete, for the histological analysis of lesions in the human brain is only rarely detailed enough to permit the identification or exclusion of deep infarctions of white matter involving connections of cortical areas other than the parietal lobules. Moreover, systematic and detailed functional testing of parietal-lobe patients is by no means a routine practice. Despite these handicaps, a clinical picture of severely debilitating agnosias, aphasias and apraxias appears well identified with parietal-lobe lesions. The widespread efferent connections of the parietal lobules considered here, in particular the evidence of a variety of neural pathways reciprocally connecting the parietal lobules with the frontal, temporal and occipital cortices, emphatically suggests a multimodal nature of the parietal-lobe mechanisms. These anatomical data suggest that the parietal lobules may serve not only to augment the potential routes of spread of somatic sensory signals from the postcentral gyrus, but also, to extend vastly the range of connections subserving communication and interaction between all sensory modalities and their motor expression.

**SUMMARY**

The efferent connections of the posterior parietal cortex were studied in rhesus monkeys subjected to selective lesions of the superior and inferior parietal lobules, which correspond approximately to Brodmann's areas 5 and 7, respectively.

Following ablations of either the superior or inferior parietal lobule, axon degeneration, stained with the Nauta and Fink-Heimer methods, was traced into the extreme, external, and internal capsules, and into the cerebral peduncle. This degeneration extended into the ipsilateral insular cortex, cingulate gyrus, prefrontal and premotor cortices, and the precentral and postcentral gyri. In addition to these connections, the superior lobule sends fibers to the ipsilateral inferior parietal lobule and superior temporal gyrus, and via the corpus callosum to the contralateral superior and inferior parietal lobules, whereas the inferior parietal lobule sends fibers to the ipsilateral superior parietal lobule and to the contralateral superior and inferior parietal lobules. A prominent fiber system to the
ipsilateral temporal lobe degenerates following lesions in the inferior parietal lobule (area 7); in such cases fiber degeneration appears in the superior, middle and inferior temporal convolutions, and in the fusiform and parahippocampal gyri.

Both lobules evidently project to the claustrum and body of the caudate nucleus. Both, moreover, have massive efferent connections with the dorsal two-thirds of the putamen. By contrast, no evidence of projections from the parietal cortex to the globus pallidus was found in any of the cases studied.

A further subcortical projection from the posterior parietal cortex involves the nucleus reticularis thalami and the nucleus lateralis posterior thalami. The inferior lobule projects directly to the nucleus lateralis dorsalis and to the mediodorsal region of the nucleus lateralis posterior that closely adjoins two thalamic cell groups: the n. lateralis dorsalis and the intralaminar nucleus centralis lateralis. The superior parietal lobule, by contrast, projects massively to a ventrolateral district of the nucleus lateralis posterior.

Parietosubthalamic connections could be traced from areas 5 and 7 to the zona incerta and fields H2 and H of Forel, but evidence for terminal connections with the n. subthalamicus (Luys) could not be found.

Both areas 5 and 7 project massively to the pretectal area and the deeper layers of the superior colliculus. This parieto-mesencephalic connection is amplified by a fiber connection from the inferior parietal lobule (area 7) to the lateral, densocellular region of the circumaqueductal gray matter. No evidence of parietal corticostriatal fiber connections was found. Finally, both parietal lobules were found to project to the pontine nuclei.

Speculations regarding the associative functions of the parietal lobules at the cortical and subcortical levels are presented, with particular emphasis upon the possible significance of the projections from the inferior parietal lobule to insular, cingulate and temporal regions of the cortex.

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REFERENCES

4. PETRAS, J. M. Unpublished observations.