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Parcellating the vertical associative fiber network of the temporoparietal area: Evidence from focused anatomic fiber dissections

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ABSTRACT

Introduction: The connectivity of the temporoparietal (TP) region has been the subject of multiple anatomical and functional studies. Its role in high cognitive functions has been primarily correlated with long association fiber connections. As a major sensory integration hub, coactivation of areas within the TP requires a stream of short association fibers running between its subregions. The latter have been the subject of a small number of recent in vivo and cadaveric studies. This has resulted in limited understanding of this network and, in certain occasions, terminology ambiguity.

Research question: To systematically study the vertical parietal and temporoparietal short association fibers.

Material and methods: Thirteen normal, adult cadaveric hemispheres, were treated with the Klinger's freeze-thaw process and their subcortical anatomy was studied using the microdissection technique.

Results: Two separate fiber layers were identified. Superficially, directly beneath the cortical u-fibers, the Stratum proprium intraparietalis (SP) was seen connecting Superior Parietal lobule and Precuneal cortical areas to inferior cortical regions of the Parietal lobe, running deep to the Intraparietal sulcus. At the same dissection level, the IPL-TP fibers were identified as a bundle connecting the Inferior Parietal lobule with posterior Temporal cortical areas. At a deeper level, parallel to the Arcuate fasciculus fibers, the SPL-TP fibers were seen connecting the Superior Parietal lobule to posterior Temporal cortical areas.

Discussion and conclusion: To our knowledge this is the first cadaveric dissection study to comprehensively study and describe of the vertical association fibers of the temporoparietal region while proposing a universal terminology.

1. Introduction

The temporoparietal (TP) region is increasingly recognized as a critical neural functional hub in contemporary neuroscientific research. This dynamic area encompasses the posterior parietal cortex (PPC), which consists of the superior parietal lobule, temporoparietal junction (TPJ), and precuneus (Precu), as well as the posterior portion of the temporal lobe. Collectively, these components contribute to the integrative functions and connectivity of the TP region within the broader neural network (Igelström et al., 2017; Uddin et al., 2010; Catani et al., 2017a).

Prior research has established connections between higher cognitive

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functions and specific components within the temporoparietal (TP) region. The successful execution of these high-level cognitive tasks necessitates the simultaneous activation of TP subregions and their integration into larger cerebral networks. Extensive investigations have elucidated the connectivity of the TP region via long-association fibers, interconnecting distant gyri within the hemisphere (Burks et al., 2017; Makris et al., 2017; Martino et al., 2013a, 2013b, 2014). However, the short vertical association fibers that interconnect adjacent gyri in subcomponents within the TP area have been insufficiently examined in the existing literature (Catani et al., 2017a; Bullock et al., 2019; De Benedictis et al., 2014a; Fernández-Miranda et al., 2008).

Recent studies have endeavored to characterize these short association fibers through in vivo and cadaveric dissections (Kamali et al., 2014a, 2014b; Panesar et al., 2019; Uesaki et al., 2018; Vergani et al., 2014; Wu et al., 2016a). Despite these efforts, a limited number of reports have resulted in terminological ambiguity and an incomplete understanding of the local network within the TP region. As such, a comprehensive investigation of these short connections is warranted to clarify the complexity of this intricate network.

The primary objective of our study is to systematically delineate the short association fibers connecting subregions within the parietal lobe, as well as the vertical parieto-temporal connections, utilizing a stepwise white matter dissection approach. By addressing the current knowledge gap and providing a detailed understanding of the local connectivity within the TP region, our study aims to enhance the scientific community's comprehension of the underlying neural architecture that supports high-level cognitive functioning.

2. Methods

Thirteen normal, adult cadaveric hemispheres (7 left hemispheres and 6 right hemispheres) were included. All hemispheres were treated with the Klinger's freeze-thaw process and their subcortical anatomy was studied using the microdissection technique (Koutsarnakis et al., 2015). Prior to dissection, the relative superficial anatomical landmarks of the parietal, occipital and frontal lobes were recorded. Hence, the Superior Parietal lobule (SPL), Supramarginal Gyrus (SMG), Angular gyrus (Ang), Pre and Post Central gyri, Superior, Middle and Inferior Occipital (SOG, MOG, and IOG respectively) and Temporal (STG, MTG, and ITG respectively) gyri, the Central sulcus, the Pre and Post Central sulci, the Intraparietal sulcus (IPS) and the External Perpendicular Fissure (EPF) were readily identified. The level of the extension of the EPF to the lateral cerebral surface was used as the posterior limit of the IPS.

Lateral to medial stepwise dissections were performed, starting from the parietal lobe and gradually extending to the frontal, occipital and posterior temporal areas. We aimed to identify the superficial and deep vertical fibers connecting parietal and temporal regions along with their cortical terminations over the lateral and medial surface. During the dissection process, long association fibers of the temporo-parieto-occipital region were identified and their relationship with adjacent short white matter fibers was recorded in detail. Medial to lateral dissections focusing on the precuneus (PreCu) and posterior third of the Cingulate gyrus (Ci) and Corpus Callosum (CC) were also included to explore the relationship of the network with deeper structures such as the white matter mass above the ventricles consisting of the Internal and External Capsule fibers merging with the Callosal fibers, termed Centrum Semiovale (CS). Four (4) hemispheres were used for coronal cuts to exhibit more clearly the spatial relationship of the regional fiber pathways.

The relevant cortical anatomy, was correlated with the termination pattern of the tracts described. The cortical areas associated with fiber terminations, were carefully documented throughout the dissection process, by color coded marking on each hemisphere (Figs. 5 and 6). In the end an overview of the termination pattern and spatial anatomy was created to facilitate understanding of the network (Fig. 7).

3. Results

3.1. Lateral to medial dissections

Upon removing the cortex and superficial U fibers of the IPS, we encountered a slim and slender group of fibers traveling along the IPS and connecting the SPL with the SMG and Ang gyri. In 9/13 of hemispheres, connections with parts of the Postcentral gyrus were, also, recognized. This fiber system was identified as Stratum Proprium Intraparietalis (SP) with its direction consistently perpendicular to the sulcus (Figs. 1A–C, 4).

Extending the superficial dissection towards the posterior temporal lobe we exposed a fine group of fibers connecting the SMG and ANG to the posterior part of the MTG and ITG respectively. This fiber layer was consistently found at the same dissection level as the SP and was classified as the short IPL-TP fiber tract (Fig. 1B).

Removing the lateral occipital U-fibers we encountered the Intrinsic Occipital Fibers (OF) running in a parallel direction as the IPL-TP and connecting regions of the SOG to the IOG. The occipito-temporal line, i.e. the imaginary line connecting the EPF and the pre-occipital notch, demarcated the transition between the OF and the short IPL-TP fiber tract (Fig. 2B).

By carefully removing the fibers of the SP and IPL-TP bundles we exposed the SLF/AF complex traversing beneath the main body of the vertical white matter tracts. Furthering the dissection towards the frontal lobe, facilitated the parcellation of these fibers. SP terminations at the SPL were identified as overlying SLF II terminations. At the level of IPL, elevation of the SP fibers uncovered SLF III terminations terminating inferiorly to the SMG and Ang. More ventrally, elevation of the IPL-TP fibers revealed AF fibers curving around the end of the Sylvian fissure (Figs. 1C,D and 2B-D).

Progressive removal of SLF II & III fibers revealed the dorsal and ventral AF fibers' curvature. At the posterior limit of the parieto-temporal junction, adjacent to the parietooccipital line, a thin group of vertical white matter fibers was identified; this tract connected superior parts of the SPL to the posterior MTG and ITG and is known as the SPL-TP fiber tract.

3.2. Medial to lateral dissection

Medial to lateral dissections were performed to exhibit the relationship between the fibers of Centrum Semiovale (CS) and the vertical association network in the area of interest. At this level, the CS consists of long association fibers stemming from the MdLF and IFOF, intermingling with axons of the Cingulum and with commissural fibers of the CC radiation. As expected, terminations of the cingulum and CC radiation at the SPL are found medial in relation to the other layers of the CS, hence medial to all vertical fibers previously described (Fig. 3).

3.3. Morphology

3.3.1. Stratum Proprium Intraparietalis

SP fibers were consistently identified as a U-shaped tract, traveling beneath the superficial arcuate fibers of the IPS. In all left and the majority of the right hemispheres (5/6 hemispheres) it could be recognized as a relatively thick and compact tract. Dorsal terminations were found along the superior bank of the IPS and the middle and lower part of the SPL. Ventral terminations were distributed along the dorsal IPL surface, namely the SMG and Ang and, in the majority of cases, to the post-Central cortices. A clear dissection plane was always present between the SP and SLF fibers, both dorsally and ventrally (Fig. 4).

3.3.2. IPL-TP

Vertical fibers seen to connect the IPL to posterior temporal regions were identified in all hemispheres. Anatomically, the fibers can be divided into two groups: an anterior group connecting the ventral-

Fig. 1. Stepwise dissection of a left hemisphere. **A:** The relative cortical anatomy is illustrated. The main sulci are marked with black dashed lines. The dotted line indicates the occipitotemporal line i. e the limit between the parietal and occipital lobe **B:** Removal of parietal and temporal u-fibers reveals the fibers of the SP (blue) and the IPL-TP (red) tracts. The inlet illustrates the fiber tracts in color, in relation to the main sulci of the area, projected in dashed line. More focused dissection on the SP is shown in Fig. 4 **C:** Elevation of the anterior part of the SP reveals the underlying fibers of the SLF traversing below the main stem of the SP. **D:** Further dissection of SP and IPL-TP to demonstrate the comparative anatomy. The posterior part of the SP and the anterior part of the IPL-TP have been retained. SLF fibers have been completely removed. The AF fibers (yellow) are seen to angle at a deeper level. A coronal cut has been performed at the level of the white line in the inlet of B and C, for better visualization of the spatial relation of the vertical TP fibers with the deeper tracts (this part of the dissection is presented in more detail in Fig. 3). **E:** After complete removal of the SP and IPL-TP the deep SPL-TP (pink) fibers are exposed traveling posteriorly to the AF, connecting the SPL to the posterior parts of the MTG and ITG. AF: Arcuate Fasciculus, Ang: Angular gyrus, Ce: Central sulcus, IPS: Intraparietal sulcus, O–Te: Occipito-temporal line, SLF: Superior Longitudinal fasciculus, SMG: Supramarginal Gyrus, SP: Stratum Proprium intraparietalis, SPL: Superior Parietal lobule.

posterior cortex of the SMG and the ventral-anterior cortex of the Ang to the posterior part of the MTG; a posterior group traveling from the ventral-posterior Ang to the posterior MTG and ITG. The anterior and posterior groups had distinct trajectory, orientation, and termination patterns, and thus are described as separate subcomponents. Terminations of the IPL-TP extended ventral to SLF terminations; a clear dissection plane was not always achieved. Temporal terminations were consistently identified as superior and posterior to AF terminations. Overall, no notable differences were observed between the left and right hemispheres (Fig. 5).

3.3.3. SPL-TP

A fine vertical fiber tract connecting the SPL to posterior temporal regions was identified in all studied specimens. SPL-TP terminations were located along the superior parts of the SPL cortex, anterior and posteriorly. Due to the thin nature of the tract, superior fiber terminations could not be consistently preserved. Temporal terminations were identified at the level of the posterior MTG and ITG cortices, traversing close to the occipitotemporal line. No Fu gyrus or occipital cortex terminations were identified. No morphological differences were recognized between the left and right hemispheres (Fig. 6).

3.4. Termination pattern

Fig. 7 illustrates the termination pattern of the association fibers along the TP area, as was revealed from our blunt dissections. Across the SPL, the SP fibers predominated ventrally with limited SLF overlap antero-inferiorly. SPL-TP terminations were located superiorly and deep to SP fibers. In each hemisphere, a small number of both SP and SPL-TP fibers were identified proximal to the medial parietal cortex, along the superior part of the precuneus cortex, and lateral to centrum semiovale fibers.

Fiber terminations along the IPL cortex display greater overlap. Dorsally, SP fibers are the main terminating fibers recognized, with a small number of SLF III terminations overlapping anteriorly. The middle part of both Ang and SMG gyri receive SLF fibers, which constitute the main terminations of the anterior IPL. The ventral part is taken up mainly by IPL-TP fibers along with lower parcellations of the SLF, however, dissection between the two was almost impossible in many instances.

Finally, both IPL-TP and SPL-TP terminations along the posterior temporal cortex were documented. The main areas of distribution were the posterior MTG and ITG. IPL-TP terminations were located superior to SPL-TP. The anterior IPL-TP group terminated usually at the posterior MTG whereas the posterior IPL-TP group dispersed along the posterior MTG and ITG cortex. No Fusiform gyrus terminations were recognized. AF fibers displayed more anterior terminations along the MTG and ITG cortex, overlapping the anterior IPL-TP fibers in 10/13 hemispheres (Fig. 7). An overview of the termination pattern can be seen in Table 1 as well.

4. Discussion

In the present study, we explored the vertical association fibers of the Temporo-Parietal area through white matter dissection. Numerous investigations have been conducted in this domain; nonetheless, their

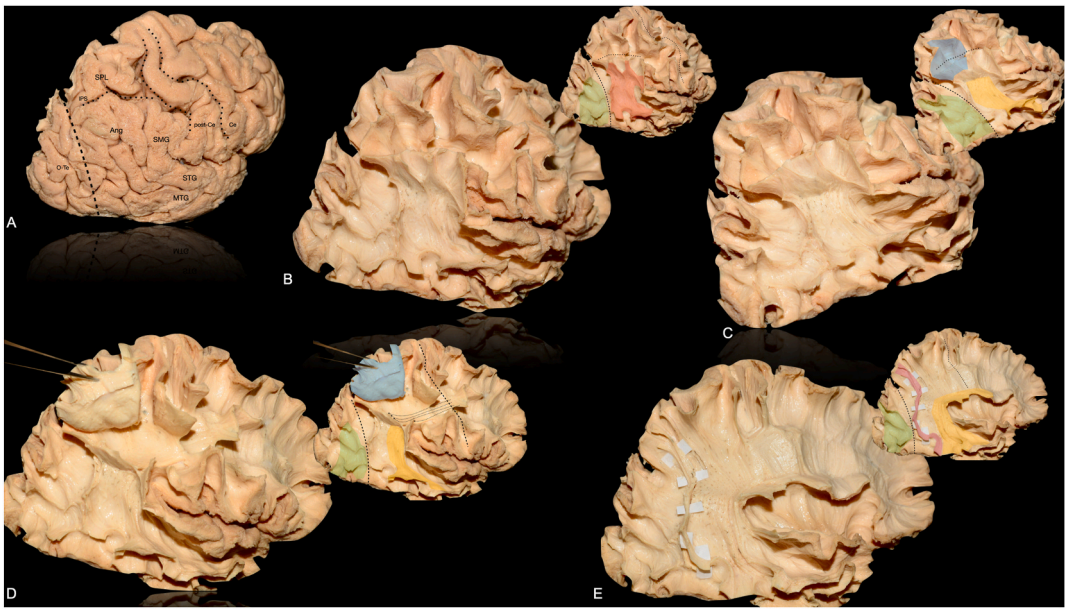

Fig. 2. Stepwise dissection of a right hemisphere. **A:** Relative cortical anatomy **B:** Removal of the occipital, parietal and posterior temporal u-fibers reveals the IPL-TP fibers (red) and the intrinsic occipital fibers (OF). The inlet shows the correlative anatomy of the IPL-TP fibers to the major sulci of the area. **C:** Removal of the IPL-TP exposes the overlapping terminations of the SP and the SLF along the IPL cortex. Inferiorly the AF fibers (yellow) are noted traversing beneath the IPL cortex. **D:** Elevation of the SP fibers isolates the SLF terminations at the IPL cortex. **E:** Removal of SLF and dorsal AF fibers, uncovers the fibers of the AF curving around the Sylvian fissure and the underlying SS fibers towards the SPL. Directly lateral to the SS, at the posterior limit of the dorsal AF fibers, the vertical fibers of the SPL-TP (pink) tract are recognized. Terminations of this tract are located at the level of the posterior MTG and ITG cortices, hence the curvature at its inferior part. AF: Arcuate Fasciculus, Ang: Angular, Ce: Central sulcus, IPL: Inferior Parietal lobule, IPS: Intraparietal sulcus, ITG: Inferior Temporal Gyrus, OF: Intrinsic Occipital Fibers, O–Te: Occipitotemporal line, post-Ce: Post-central sulcus, SLF: Superior Longitudinal fasciculus, SMG: Supramarginal Gyrus, SP: Stratum Proprium intraparietalis, SPL: Superior Parietal lobule.

primary emphasis has been on long association fibers, often neglecting the presence of short fibers or dismissing them as subsidiary components of the principal tracts within the cerebral hemisphere. This selective focus has led to an incomplete understanding of the intricate organization and connectivity of the area's white matter architecture. (Martino et al., 2013c; De Benedictis et al., 2014b; Baker et al., 2018). Tractography studies have attempted to describe superficial white matter tracts of the brain, including fibers in the TP area (Kamali et al., 2014a, 2014c; Panesar et al., 2019; Uesaki et al., 2018; Makris et al., 2004; Catani et al., 2005a, 2017b; Oishi et al., 2008; Wu et al., 2016b; Lin et al., 2020). To the best of our knowledge, we believe that our study represents the first dissection-based investigation specifically concentrating on these fibers.

In the most superficial layer, immediately beneath the superficial U-fibers, we identified two distinct fiber sets. One is a U-shaped intraparietal tract traversing the depth of the IPS, termed the Stratum Proprium Intraparietalis. These fibers have been reliably reconstructed in previous tractography investigations. (Uesaki et al., 2018; Catani et al., 2017b; Oishi et al., 2008). At the same dissection level, we identified and examined a second association tract system extending between the IPL and posterior temporal areas. This fiber system has been a subject of terminological debate in recent literature, with various taxonomic classifications proposed. We selected the terminology proposed by Kamali et al. as the term IPL-TP was deemed more appropriate for describing these fibers (Bullock et al., 2019; Kamali et al., 2014c). At a deeper level, we observed a slender, vertically oriented white matter layer extending between the SPL and posterior temporal areas. Recent tractography studies have referred to this tract as the SPL-TP. (Kamali et al., 2014c; Oishi et al., 2008; Wu et al., 2016b).

The vertical association fibers were consistently identified lateral to the internal capsule and callosal fibers. For each tract, we formed a detailed map of their trajectory and termination pattern across the cortex of the lateral surface. Additionally, we thoroughly examined and documented their spatial relationship with the long-association fibers in the region. Our analysis suggests a distinction in the termination patterns and fiber trajectories of the described fibers, particularly in their relation to longer association tracts such as the SLF or AF. His analysis could support the notion that these vertical tracts exist as distinct anatomically structures, rather than mere subcomponents of the larger fiber systems. (De Benedictis et al., 2014b; Baker et al., 2018). However, this interpretation is subject to the limitations of our current methodologies and the inherent complexity of neural fiber architecture. Further research is needed to conclusively determine the extent of their anatomical and functional independence.

4.1. *Stratum proprium intraparietalis*

Within the parietal lobe, at the depth of the IPS, a compact fiber tract was identified connecting the cortex of the SPL to the IPL. First described by Sachs in 1892 (Vergani et al., 2014), this tract was initially recreated via tractography by Oishi et al. as an SP-parietotemporal blade, recognized in macaque and human brains (Oishi et al., 2008). Vergani et al. briefly acknowledge the tract in their investigation of the intralobar fibers of the occipital lobe, without delving into a more detailed analysis of its characteristics. (Vergani et al., 2014). A comprehensive tractographic description by Uesaki et al. details fibers terminating at the supramarginal gyrus (SMG), parietal operculum, and posterior end of the Sylvian fissure. However, the literature does not report any terminations in the Ang. (Uesaki et al., 2018). In our study, we found terminations along the dorsal cortex of the Ang gyrus as well as the SMG and Post-Ce gyri, which constitute the parietal operculum. All SMG terminations were limited to the dorsal surface of the gyrus. Dorsomedial terminations were recognized along the SPL and Precu, consistent with previous descriptions (Uesaki et al., 2018). In our study, the main stem of the tract closely resembles the "Parietal Inferior to Superior" tract described by Catani. The subcomponents "Parietal - Inferior to Post--central" and "Parietal - Superior to Postcentral" also exhibit similar termination patterns to the SP, in the postcentral cortex. Catani et al.'s study offers a more detailed anatomo-imaging depiction of the short

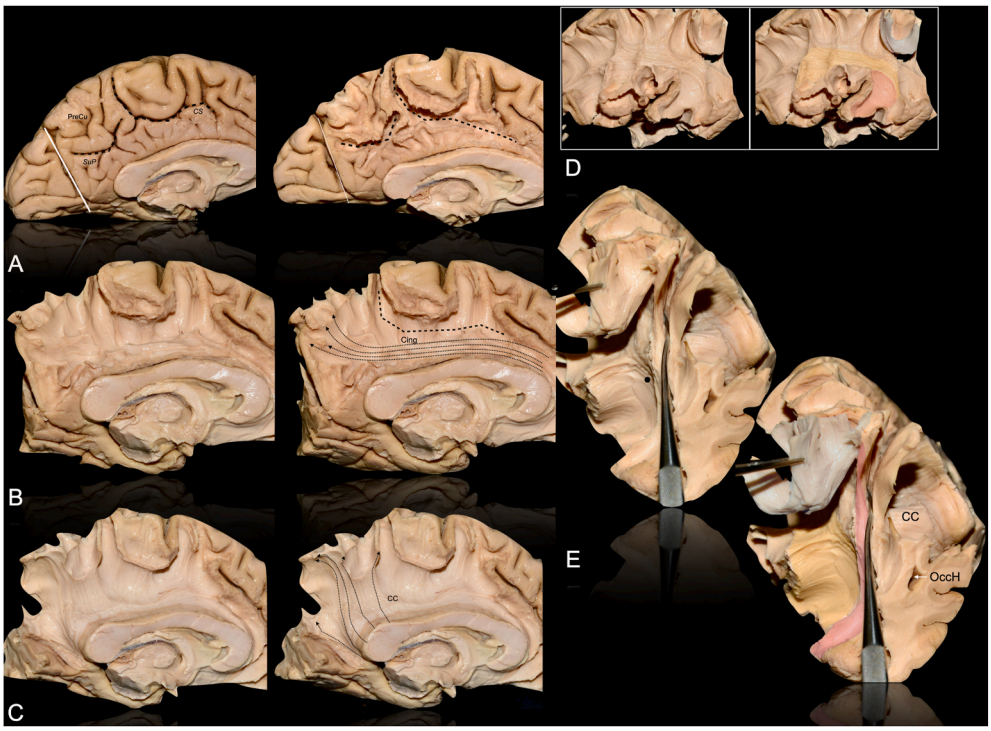

Fig. 3. Medial stepwise dissection. After dissection of the lateral surface as was shown in previous images, the same hemisphere was used to perform medial to lateral dissection. Special attention was given to the parietal termination pattern of the medial fiber tracts. **A:** Relative cortical anatomy and u-fiber anatomy after removal of the cortex. **B:** After u-fiber removal the cingulum radiation is exposed terminating at the middle and superior parts of the Precuneus. **C:** Removal of the cingulum fibers reveals the CC fibers radiating towards the superior part of the precuneus, intermingling with the fibers of the corona radiata. **D:** Lateral view of the hemisphere at this stage of the dissection. The SLF has been removed and the posterior part of the SP has been elevated and illustrated in blue, revealing the underlying fibers of the AF and the IPL-TP (red). **E:** Coronal view illustrating the relationship between the fiber tracts of the medial surface and the vertical temporoparietal tracts. The SP terminates antero-lateral to the CeS. The SPL-TP (pink) is the last vertical fiber tract above the CS fibers. The CC fibers constantly terminate medial to all fibers, displaying a clear anatomical cleavage plane, as is demonstrated. AF: Arcuate Fasciculus, Ang: Angular, CC: Corpus Callosum, Ce: Central sulcus, Cing: Cingulate sulcus, CR: Corona Radiata, CS: Centrum Semiovale, IPL: Inferior Parietal lobule, IPS: Intraparietal sulcus, ITG: Inferior Temporal Gyrus, OccH: Occipital Horn, PreCu: Precuneus, SLF: Superior Longitudinal fasciculus, SMG: Supramarginal Gyrus, SP: Stratum Proprium intraparietalis, SPL: Superior Parietal lobule, SuP: Subparietal sulcus.

parietal lobe connections, categorizing fibers into multiple subcomponents based on their connected gyri, with a particular emphasis on SPL connections. (Catani et al., 2017b). We opted not to adopt this taxonomic system, as it was considered overly complex for our study's scope and did not encompass parieto-temporal connections.

The spatial relationship of the SP with neighboring tracts was also studied. Previous descriptions placed it close to the AF fibers (Uesaki et al., 2018). In our study, we consistently observed the SP fibers directly above the SLF fibers, while the AF fibers were situated deeper to the SLF fibers. Furthermore, we identified the OF fibers in all hemispheres as a distinct fiber system connecting the superior and inferior occipital regions, using the occipitotemporal line as a demarcation point. These findings align with previous investigations of occipital intralobar fibers. (Vergani et al., 2014). To the best of our knowledge, this is the first detailed dissection study of the SP fasciculus.

4.2. TP-IPL

Along the ventral cortex of the IPL, 2 groups of vertical fibers were identified extending between the SMG and Ang to posterior Temporal areas. This fiber system has been described in the literature with various names. Initial descriptions categorized it as part of the AF (Makris et al., 2004; Catani et al., 2005a, 2008; Turken et al., 2011). Oishi et al. confirmed the presence of vertical fibers in the area in humans and macaques (Oishi et al., 2008). As the examination of the AF/SLF complex evolved toward a more refined characterization of the two fiber systems, the vertical fibers between the IPL and posterior temporal cortex were subsequently described as a component of the SLF system. Terms as SLF-V (Wu et al., 2016b; Lawes et al., 2008; Martino et al., 2012), posterior SLF (Martino et al., 2012), perisylvian SLF (Martino et al., 2012; Catani et al., 2005b) and vertical SLF (Martino et al., 2013c) have been introduced. Interestingly, Kamali et al. described this tract as separate from the SLF/AF system, with the name IPL-TP (Kamali et al., 2014a, 2014c), followed by Panesar et al. who used the term "Temporo-Parietal Aslant tract" and also considered the fibers separate from the AF complex (Panesar et al., 2019). The tractography study by Kamali et al. concentrated on the connectivity of the temporo-parietal area tracts, offering more consistent and unambiguous terminology, which was considered better suited for the purposes of the current investigation.

In our study, the anterior group of fibers was observed to extend from the ventral SMG and ventral-anterior Ang to the posterior MTG cortex. Conversely, the posterior group spanned from the ventral-posterior Ang to the MTG and ITG cortices. This characterization differs from Kamali et al.'s description, in which the IPL-TP is reported to connect the SMG and Ang to the STG and MTG, respectively. (Kamali et al., 2014a, 2014c). Wu et al. propose a taxonomy with SLF-V SMG and SLF-V Ang terminating in MTG and ITG, near the AF origin (Wu et al., 2016b). Bullock et al. reintroduce the term "posterior Arcuate" for these fibers, considering them part of the AF (Bullock et al., 2019). Panesar et al. describe a similar pattern, naming the separate fiber system from the SLF/AF complex as "temporoparietal aslant tract (TPAT) (Panesar et al., 2019).

In our study, we did not identify SMG fibers terminating in the ITG as

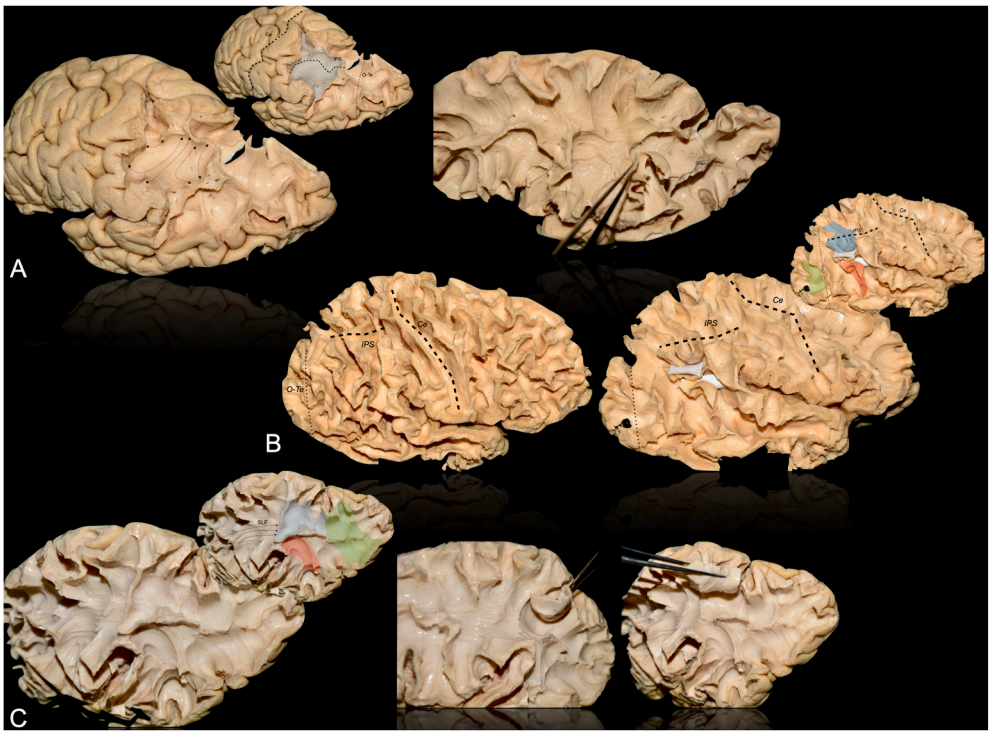

Fig. 4. Morphology, termination pattern and spatial relationship of the SP fiber bundle. **A:** Dissection steps of a left hemisphere. *Left image:* SP bundle as it extends along the depth of the IPS. Terminations of the tract can be recognized along the dorsal SMG and Ang cortices, the Post-Ce gyrus, forming the inferior bank of the IPS; and the inferior SPL, forming the superior bank of the IPS. The inlet shows the fibers in blue, maintaining the color coding of previous images. *Right image:* SP fibers are elevated with the forceps, revealing the underlying SLF fibers. **B:** Dissection steps of a right sided hemisphere. *Left image:* shows the relative anatomy after removal of the cortex. The main sulci of the area, namely the IPS and the Ce, are illustrated with dashed lines. *Right image:* The u fibers have been removed and the TP and IPL-TP fibers have been elevated from the SLF using thin white cartons. It is evident that both fibers are at the same dissection level, with their terminations being separated by the SLF fibers at the mid level of the IPL. The inlet illustrates the fiber tracts in color, in relation to the main sulci. **C:** Dissection steps of a left sided hemisphere. *Left image:* Correlative anatomy of the fibers of the TP area is shown. The SP and IPL-TP are at the same dissection level. The SLF fibers are shown in arrows to dive beneath the SP fibers, towards their IPL terminations. The AF fibers are seen to emerge at a deeper level than the SLF terminations and the IPL-TP fibers. The OF fibers are shown to traverse vertically the occipital lobe. All fibers are illustrated in the inlet, retaining the color coding of previous figures. *Right image:* Mirror images of the same hemisphere. The SP fibers are elevated with the foprceps. Anterior view (left) showing the SLF fibers passing beneath the SP and terminating at the IPL. Superior view (right) showing the SLF terminations at the IPL after SP elevation with the forceps. IPL-TP fibers run at a more superficial level and the AF fibers emerge at a deeper level, beneath the SLF terminations. AF: Arcuate Fasciculus, Ce: Central sulcus, IPS: Intraparietal sulcus, SLF: Superior Longitudinal fasciculus.

described by Wu et al. (2016b). All IPL-TP fibers were found ventrally in the IPL cortex, below SLF III terminations. A clear dissection plane for IPL terminations was not always discernible, possibly causing discrepancies with Bullock et al.'s description (Bullock et al., 2019). Our findings mostly align with the TPAT description, but we chose Kamali et al.'s terminology for previously explained reasons (Kamali et al., 2014a, 2014c; Panesar et al., 2019).

IPL-TP fibers were consistently observed directly beneath superficial u-fibers and lateral to AF fibers, in line with previous descriptions (Kamali et al., 2014a, 2014c; Panesar et al., 2019; Wu et al., 2016b). During dissections, IPL-TP fibers appeared at the same level as SP, beneath SLF terminations in the IPL cortex. AF fibers were visible after removing SLF and IPL-TP fibers, with a clear dissection plane. We believe IPL-TP is structurally distinct from the SLF/AF complex and warrants a separate description. No overlap with the OF was observed, consistent with prior reports (Panesar et al., 2019; Vergani et al., 2014).

4.3. SPL-TP

Initial tractographic descriptions identified long U-shaped fibers extending from the posterior SPL to the temporal cortex below the Ang gyrus (Oishi et al., 2008). Kamali et al. and Wu et al. observed a fiber bundle connecting anterior SPL cortex with temporal areas, with cranial fibers near MdLF terminations on the SPL cortex and caudal fibers along MTG and ITG cortex. Wu et al. reported connectivity with the Fusiform gyrus, ITG-IOG intersection (Kamali et al., 2014c; Wu et al., 2016b). Bullock et al. located superior terminations medial to IPS cortex and ventral terminations at MTG, ITG, and Fu gyrus without occipital involvement (Bullock et al., 2019). Our study, the first to provide dissection data, confirmed this fine fiber tract's existence, with dorsal terminations at the SPL cortex and caudal terminations in posterior temporal areas, excluding occipital or Fusiform cortex. The presence of additional fibers connecting these areas cannot be definitively ruled out due to the tract's fine shape.

Our findings concur with existing data on the tract's shape and spatial relationship with surrounding fibers. Positioned deep to SLF II fibers, it lies directly lateral to MdLF and IFOF fibers (Bullock et al., 2019; Kamali et al., 2014c; Wu et al., 2016b). The dorsal part of the AF runs parallel and more anteriorly at the same level, while the OF tracts follow a more lateral and posterior trajectory, parallel to the SPL-TP (Kamali et al., 2014c; Wu et al., 2016b).

4.4. From the "canon" to the vertical association system

Historically, Meynert described association fibers as having an anteroposterior orientation, a concept that became established through dissection studies and guided subsequent research (Bullock et al., 2019). Consequently, connectivity studies in regions like the TPj tended to focus on these long tracts, overlooking vertical fibers (Catani et al., 2017a; Bullock et al., 2019; De Benedictis et al., 2014a). Recent

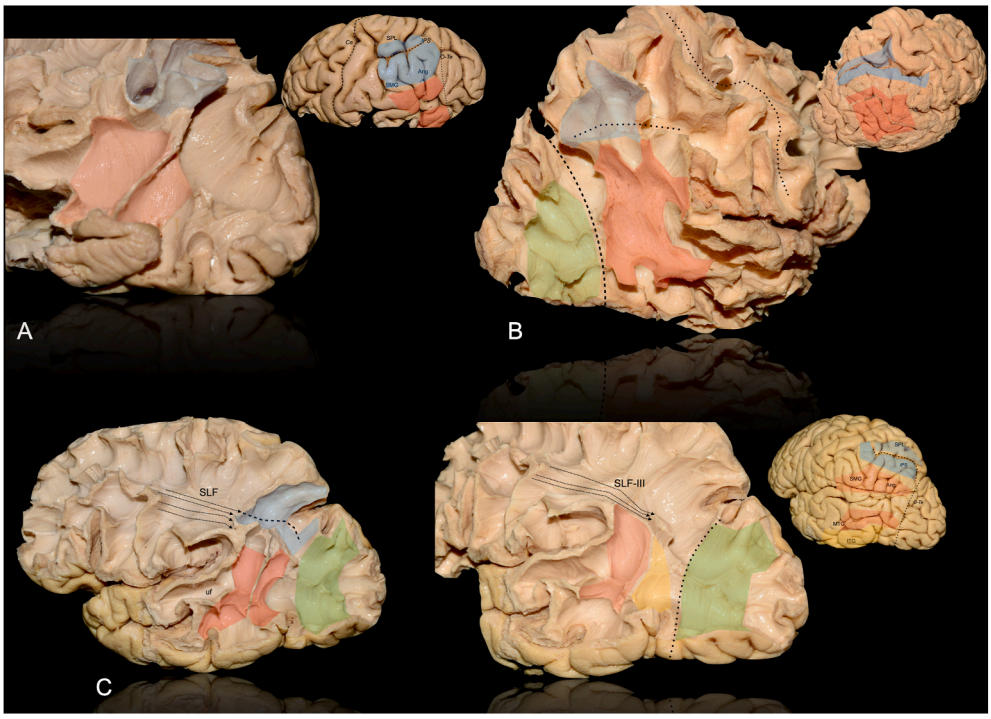

Fig. 5. Morphology, termination pattern and spatial relationship of the IPL-TP fiber bundle. **A:** Dissection steps of a left-sided hemisphere. The anterior and posterior group of IPL-TP fibers. Superiorly the SP fibers have been dissected as well. The color coding from previous images has been retained (SP: blue, IPL-TP: red). The two groups show different trajectory and termination pattern. The anterior group extends between the SMG and anterior Ang gyro to the MTG, whereas the posterior group, in this hemisphere, extends between the posterior Ang and the posterio MTG. The inlet shows the projection of the terminations to the cortex of the hemisphere. The IPS can be identified running horizontally from the midpoint of the post-Central sulcus. The blue terminations, representing SP, are shown to cover the banks along the IPS, as a connection between SPL and IPL. The red terminations cover the ventral part of the IPL (SMG & Ang) and terminate at posterior temporal cortical areas towards the caudal part of the hemisphere. B: Dissection steps of a right-sided hemisphere. The IPL-TP is shown to extend between the IPL and the posterior temporal gyrus. The anterior and posterior groups are not so clearly demarcated in this hemisphere. The termination pattern is similar to the previous hemisphere. Fibers from the posterior group are seen to terminate at the posterior ITG. The inlet shows the termination projection to the cortex. Again in blue, we see the SP fibers along both sides of the IPS and with red we see the extent of the IPL-TP fibers along the cortex posterior and inferior to the termination of the Sylvian fissure, representing the IPL and posterior temporal areas, respectively. **C:** Dissection steps of a left-sided hemisphere. *Left image:* The anterior and posterior groups are shown in red, exerting an almost opposite curvature among them. Also, the SP fibers are shown in blue at the depth of the IPS (dotted line). Note the SLF fibers (arrows) anteriorly and the VO fibers (green) posteriorly. It is evident that the IPL-TP is a structurally separate fiber tract from its neighboring vertical association fibers. *Right image:* The posterior group has been removed, revealing the underlying AF fibers (yellow), emerging from a deeper level, towards the ITG. The inlet shows the same termination pattern as before. In this hemisphere, we can appreciate the different termination pattern between the IPL-Tp and AF. The AF fibers terminate deeper and more anteriorly at the posterior temporal cortex. AF: Arcuate Fasciculus, Ang: Angular gyrus, Ce: Central sulcus, IPS: Intraparietal sulcus, O–Te: Occipito-temporal line, SLF: Superior Longitudinal fasciculus, SMG: Supramarginal Gyrus, SP: Stratum Proprium intraparietalis, SPL: Superior Parietal lobule, STG: Superior Temporal gyrus, MTG: Middle Temporal gyrus.

investigations into vertical tracts such as the Frontal Aslant Tract (FAT) and the Vertical Occipital (VO) fasciculus (Kamali et al., 2014a, 2014c; Vergani et al., 2014; Oishi et al., 2008; Catani et al., 2012, 2013) have introduced the concept of a vertical association system, challenging the traditional view and providing a foundation for studying "non-canonical" fibers (Bullock et al., 2019).

Mandonnet et al. proposed a universal taxonomy system for association tracts based on fiber location and orientation (Mandonnet et al., 2018), which has been reproduced in later studies (Porto de Oliveira et al., 2021). They introduced three groups for vertical fibers: one anterior and two posterior transverse systems (ATS and PTS, respectively). The anterior group involves the FAT, which has been extensively described (Catani et al., 2012; Aron et al., 2007; Thiebaut de Schotten et al., 2012; Szmuda et al., 2017; Koutsarnakis et al., 2017; Ookawa et al., 2017; Briggs et al., 2018; Burkhardt et al., 2021). The posterior groups, PTS-I and PTS-II, encompass the temporoparietal vertical association fibers and the VO fasciculus, respectively. To our knowledge, this study presents the first comprehensive description of the PTS-I group of fibers, adopting terminology based on the principles of Mandonnet et al.'s taxonomy system.

4.5. Functional correlation and surgical implications

Functional studies associate the dominant temporoparietal area with auditory speech comprehension, semantics, and conceptual aspects, primarily through the long association fibers of the SLF/AF complex (Porto de Oliveira et al., 2021; Sarubbo et al., 2015; Catani et al., 2014). Disruption of these fibers within the semantic pathway of speech (Hickok et al., 2004) results in anomia (Sarubbo et al., 2015) and alexia (Sarubbo et al., 2015). In contrast, the non-dominant hemisphere is involved in auditory-spatial processing (Zemmoura et al., 2015), attention, and visuospatial cognition (Barrick et al., 2007), with damage potentially leading to spatial neglect (Nakajima et al., 2020).

Intra-operative stimulation of the area has elicited vestibular symptoms, such as nystagmus and vertigo (Fernández-Miranda et al., 2008; Spena et al., 2006), and perceptual spatial neglect (Nakajima et al., 2020). Direct stimulation of the right angular (Ang) cortex and the subcortical white matter has induced out-of-body experiences (OBEs) and illusory hand transformations (Blanke, 2012; Blondiaux et al., 2021; Ventre-Dominey, 2014). The temporoparietal area has been linked to self-processing and body self-consciousness (Blanke, 2012; Blondiaux et al., 2021; Ventre-Dominey, 2014).

Co-activation of regions like the IPS, PMC, Post-Central, and medial

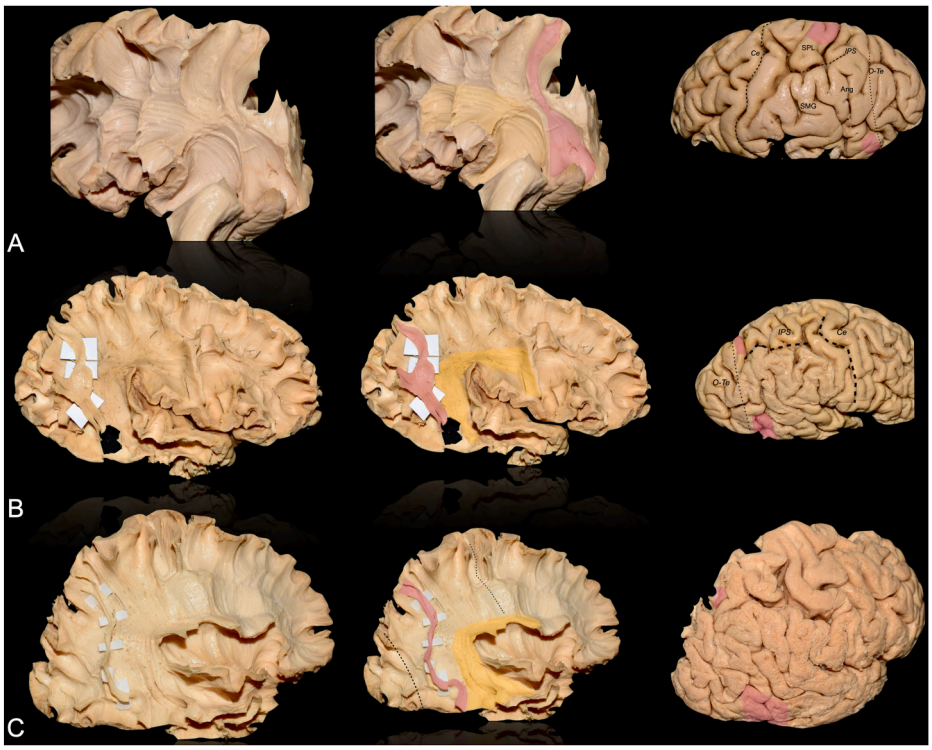

Fig. 6. Morphology, termination pattern and spatial relationship of the SPL-TP fiber bundle. The left image shows the unedited dissection image, the middle image shows the color mapping of the fibers and the right image shows the cortex projection of the fiber terminations as were recorded in each hemisphere. The same color-coding has been retained. **A:** Dissection step of a left-sided hemisphere (this hemisphere was used for medial dissections, hence the occipital lobe has been removed, as was shown in Fig. 1). The SPL-TP is shown to extend between the mid-anterior part of the SPL cortex (close to the post-central sulcus) to the ITG cortex. The bundle extends clearly dorsal to the AF fibers. The difference in its thickness between the superior and the inferior part is attributed to the thin nature of the bundle, resulting in frailty of the fibers during dissection. **B:** Dissection step of a right-sided hemisphere. The SPL-TP extends from the posterior part of the SPL, almost adjacent to the occipito-temporal line, to the posterior MTG and ITG. The bundle has been elevated with thin white paper pieces, to emphasize its difference from the AF fibers. **C:** Dissection step of a right-sided hemisphere. The SPL-TP extends from the middle part of the SPL cortex to the posterior MTG and ITG cortices, forming a curvature at its inferiormost part. In all images we can appreciate the termination pattern of the bundle. Along the SPL, the fibers can be seen at the superior-most part of the lobule and caudally we can appreciate the fibers terminating along the postero-inferior MGT and the ITG, remaining separate from the AF terminations. In all insets we can appreciate the coloured areas remaining clearly anterior to the O–Te line, indicating their role as a Parieto-Temporal connection. Ang: Angular gyrus, Ce: Central sulcus, IPS: Intraparietal sulcus, O–Te: Occipito-temporal line, SMG: Supramarginal Gyrus, SPL: Superior Parietal lobule.

Parietal form an important component of the network responsible for the body self-consciousness (Blanke, 2012). A recent lesion overlap analysis associated autoscopic phenomena (AP) with focal lesions such as vascular tumors, AVMs, and focal epilepsy. The map of disrupted networks involves mainly the TP area and adjacent regions, resembling the vertical temporoparietal tracts described in this study; only small clusters in more distant areas like the parahippocampal/hippocampus, IFG and insula were identified (Blondiaux et al., 2021).

With the temporoparietal junction (TPj) at the center of multisensory processing, the recruitment of adjacent regions (precuneus, ITG, and IFG) completes the network (Blondiaux et al., 2021; Ventre-Dominey, 2014). The TP areas (mainly supramarginal gyrus (SMG) and Ang) play a central role in vestibular processing and OBE occurrence, co-activating with neighboring regions like STG and ITG (Blondiaux et al., 2021; Ionta et al., 2011; Vogeley et al., 2004). Visuospatial and self-related processing involve co-activation of precuneus with TP areas (Blondiaux et al., 2021; De Ridder et al., 2007; Cavanna et al., 2006; Northoff et al., 2006). Functional connections between the precuneus/superior parietal lobule (SPL) and posterior parts of the ITG have been implicated in own-face recognition, self-location, and self-perception (Blondiaux et al., 2021; Cavanna et al., 2006; Allison et al., 1994; Ungerleider et al., 1994; Conway, 2018).

In patients with seizures originating from the parietal lobe, interictal electroencephalogram (EEG) findings display a variable distribution pattern extending to neighboring lobes, including frontal and temporal regions. Interestingly, there is a reduced incidence of bilateral activation when compared to other epilepsy subtypes (Ristić et al., 2012). These epileptic events may manifest with a diverse array of symptoms, such as sensory and auditory disturbances (e.g., dysesthesias, vertigo), or autoscopic phenomena (AP) (Salanova, 2012). In the latter scenario, patients often report experiencing multiple types of autoscopic phenomena (AP) during an episode or even postictal (Blondiaux et al., 2021; Maillard et al., 2004; Tadokoro et al., 2006). Therefore, a focal network within the temporoparietal region, as detailed in our study, may signify the underlying distribution pathway for these focal seizures, offering potential targets for future therapeutic interventions in treatment-resistant cases.

The literature places the posterior parietal cortex and its functional connections at the center of the network mediating body self-consciousness and autoscopic phenomena. The anatomical connectivity network described in this study corresponds with these functional findings. Consequently, disruption of the vertical TP network might contribute to autoscopic phenomena and the formation of body self-consciousness. White matter dissection is a purely anatomical study and cannot provide definitive functional data, which is one of the limitations of the technique. In order to dissect and study a fiber tract, the overlying structures need to be elevated or removed. Thus, the termination overlaps, even when cortex sparing technique is employed (Martino et al., 2011), as well as the spatial relationship between adjacent fibers is to an extent observer-dependent (Jitsuishi et al., 2020). This can be limited with the increasing experience in white matter dissection and detailed documentation of every step. In the present

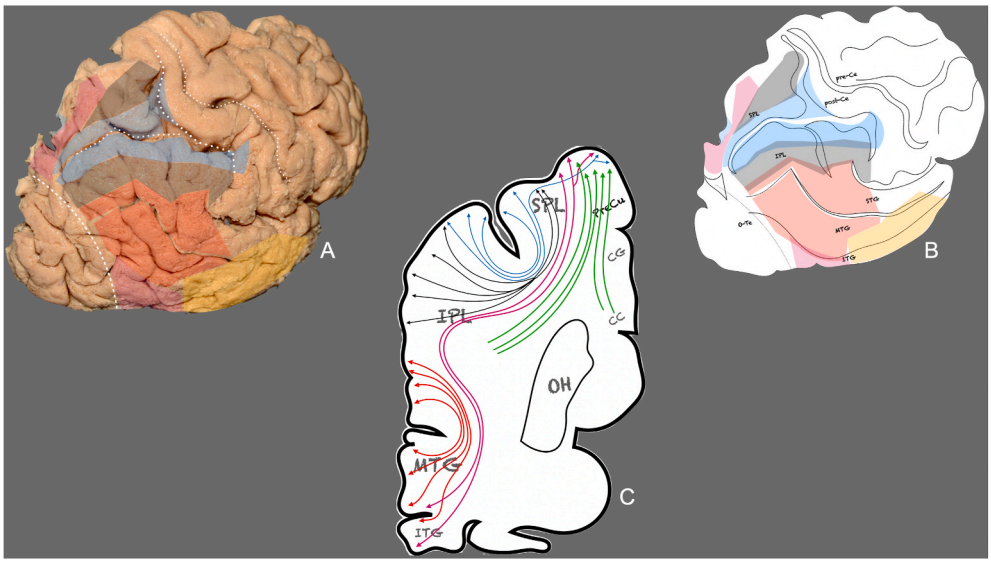

Fig. 7. Map of the tracts in the TP area. **7A:** Projection of the terminations along the Precu, SPL, IPL and posterior temporal cortex, in one of the dissected hemispheres. Color coding is the same as the previous images (blue: SP, grey: SLF, red: IPL-TP, pink: SPL-TP, yellow: AF, green: CR). **7B:** Cumulative illustration of the terminations as was recorded in all hemispheres used in the present study. There is marked overlap between the SLF and SP in the SPL and SFL and IPL-TP along the IPL cortex. **7C:** Schematic illustration of the spatial relationships and termination pattern of the short association fibers in a coronal cut of the Parietal lobe. The short association fibers can be seen clearly lateral to the Corona Radiata fibers. Ang: Angular gyrus,CC: Corpus Callosum, C: Cingulate gyrus, CR Corona Radiata, IPL: Inferior Parietal lobule, ITG: Inferior Temporal Gyrus, MTG: Middle Temporal gyrus, OH: Occipital Horn, O–Te: Occipito-temporal line, post-Ce: post-central gyrus, pre-Ce: pre-central gyrus, PreCu: Precuneus, SMG: Supramarginal Gyrus, SP: Stratum Proprium intraparietalis, SPL: Superior Parietal lobule, STG: Superior Temporal gyrus, MTG: Middle Temporal gyrus.

Table 1
Overview of termination pattern of vertical association fibers of the temporoparietal lobe.

Fascicle	Dorsal termination	Ventral termination	Termination Overlap
Stratum proprium Intraparietalis (SP)	Ventral SPL	Dorsal Ang	Dorsal: SPL-TP & SLF
	Superior bank of IPS	Dorsal SMG	
	Post-Central (above IPS)	Post-Central (below IPS)	
	PreCu		Ventral: SLF
IPL-TP	Ventral ANG	Posterior MTG + ITG	Dorsal: SLF
	Ventral SMG	Posterior MTG	Ventral: SPL-TP AF
SPL-TP	Dorsal SPL	Posterior MTG + ITG	Dorsal: SP Ventral: IPL-TP

AF: Arcuate Fasciculus, Ang: Angular gyrus, IPL: Inferior Parietal lobule, IPS: Intraparietal sulcus, ITG: Inferior Temporal Gyrus, MTG: Middle Temporal gyrus, PreCu: Precuneus, SLF: Superior Longitudinal fasciculus, SMG: Supramarginal Gyrus, SP: Stratum Proprium intraparietalis, SPL: Superior Parietal lobule, STG: Superior Temporal gyrus.

study, the overlap between the functional and anatomical network, as they were described, cannot be ignored. Further investigation requires focused studies using functional connectivity data from imaging and direct stimulation under neuropsychological testing.

5. Conclusion

In this investigation, the authors sought to examine the morphological characteristics and connectivity patterns of the subcortical structures within a region that has been largely underexplored. The findings of this study offer conclusive evidence regarding the existence of the vertical association fiber system in the temporoparietal (TP) area and provide insights into the terminological complexities surrounding this structure. To elucidate the functional implications of this fiber system and its potential role in body self-consciousness or other higher-order cognitive processes, additional research is warranted.

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Author contributions

Conception and design/acquisition of data: ED, AVK, CK; Analysis and interpretation: ED, AVK, CK, SK, EL; Drafting the article: ED, AVK, SK, CK; Critically revising: ED, AVK, CK, SK, TT, GS, EN, TK, GPS, EH, LA, VP; Final approval: all authors.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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