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ORIGINAL ARTICLE

Anatomy and white matter connections of the lateral occipital cortex

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Abstract
Purpose White matter tracts link different regions of the brain, and the known functions of those interconnected regions may offer clues about the roles that white matter tracts play in information relay. The authors of this report discuss the structure and function of the lateral occipital lobe and how the lateral occipital lobe communicates with other regions via white matter tracts.
Methods The authors used generalized q-sampling imaging and cadaveric brain dissections to uncover the subcortical white matter connections of the lateral occipital lobe. The authors created GQI of ten healthy controls and dissected ten cadaveric brains.
Results The middle longitudinal fasciculus, vertical occipital fasciculus, inferior fronto-occipital fasciculus, inferior longitudinal fasciculus, optic radiations, and a diverse array of U-shaped fibers connect the lateral occipital lobe to itself, parts of the temporal, parietal, and medial occipital cortices. The complex functional processes attributed to the lateral occipital lobe, including object recognition, facial recognition, and motion perception are likely related to the subcortical white matter tracts described within this study.
Conclusions There was good concordance between the white matter tracts generated using GQI and the white matter tracts that were found after dissection of the cadaveric brains. This article presents the anatomic connections of the lateral occipital lobe and discusses the associated functions.

Keywords Anatomy · DSI · Occipital lobe · Tractography · White matter

Introduction

The occipital lobe has a significant role in visuospatial cognition. The dorsal and ventral streams are essential for spatial location and object recognition, respectively. The white matter tracts that connect the occipital lobe to itself, the frontal, parietal, and temporal lobes are vital for information transfer. During surgery (such as awake craniotomy), these tracts must be avoided to preserve neurological function [8, 28]. For example, if the middle longitudinal fasciculus (MdLF) is damaged, the patient could potentially have problems with language processing.

The occipital lobe is divided into medial and lateral regions. The lateral occipital lobe lies within the posterior portion of the skull. The anterior border separating the occipital lobe from the parietal and temporal lobes is the lateral parieto-temporal line, which extends from the preoccipital notch to the parieto-occipital sulcus. The tentorium cerebelli forms the inferior border. The lateral occipital lobe continues superiorly, until reaching the cuneus along the medial side. It continues inferiorly until reaching the occipito-temporal sulcus medially, which separates it from the fusiform gyrus.

Visual processing in the cerebral cortex is thought to occur according to a two-stream model, consisting of dorsal and ventral visual streams [18]. The dorsal stream extends from visual area 1 (V1) to the posterior parietal area, and is associated with the visuospatial coordination of objects [17, 22]. The ventral stream extends from V1 to the temporal

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cortex and is associated with object recognition [7, 17]. Some have proposed that these two streams are interconnected to facilitate complex behavior [12, 41]. Though the works of Rokem et al., a more detailed understanding of the communication between the dorsal and ventral stream was established [6, 40]. This work emphasizes the importance of understanding white matter tracts that are linked to brain gyri with visual functionality.

The lateral occipital lobe has functional associations with the dorsal and ventral visual streams [17, 18, 53]. The white matter connections that create this functional association have been investigated in the past. The vertical occipital fasciculus was originally discovered by Wernicke through dissection in monkeys (1881) and was subsequently identified in human studies by Obersteiner (1888) [53]. Similarly, Seltzer et al. described the middle longitudinal fasciculus (MdLF) of rhesus monkeys in 1984. A better understanding of the structural connections integrated within the lateral occipital lobe may help explain its role in visual processing.

In this study, we used deterministic fiber tractography paired with cadaveric brain dissection serving as ground truth to describe the subcortical white matter anatomy of the lateral occipital lobe. Fiber tractography was performed prior to dissection and served as a guide for the dissection of all relevant white matter tracts. Our goal was to perform a structural analysis of the lateral occipital lobe and relate these findings to the functional processes associated with this part of the cerebral cortex.

Materials and methods

All work related to this project was performed at the University of Oklahoma Health Sciences Center. Permission was obtained from the appropriate entities before proceeding with the material presented in this project. There is no identifiable information presented within this report.

Definition of region of interest

The lateral occipital lobe is within the posterior portion of the skull. The anterior border (separating it from the parietal and temporal lobes) is the lateral parieto-temporal line, which connects the preoccipital notch to the parieto-occipital sulcus. The tentorium cerebelli forms the inferior border. The medial border is the cuneus superiorly and the occipito-temporal sulcus inferiorly (which separates it from the fusiform gyrus).

The most comprehensive definition of the lateral occipital lobe comes from Alves et al. [1]. The authors described the lateral occipital lobe using a three-gyrus model. The superior occipital gyrus was demarcated as the gyrus above the intra-occipital sulcus (the portion of the intra-parietal sulcus past the parieto-occipital line). It extends to the medial portion of the occipital lobe where it continues as the cuneus on the medial portion of the occipital lobe. The middle occipital gyrus was described as the area between the intraocccipital sulcus (below the transverse occipital sulcus) and the lateral occipital sulcus (which is nearly continuous with the superior temporal sulcus). The medial occipital gyrus is adjacent to the posterior portion of the angular gyrus. The inferior occipital gyrus was demarcated as the area inferior to the lateral occipital sulcus. The inferior occipital gyrus abuts the posterior portion of the middle temporal gyrus. The occipital and parieto-temporal gyri are roughly divided by the lateral parieto-temporal line. To ensure consistency, these anatomic definitions were adopted for the purposes of performing deterministic tractography and cadaveric brain dissection. The sulci and gyri of the lateral occipital lobe are demonstrated in Fig. 1.

GQI tractography

Imaging data from the Human Connectome Project (HCP) was obtained for this study from the HCP database (http://humanconnectome.org, release Q3). Diffusion imaging from ten healthy adult controls was analyzed: 100,307, 103,414, 105,115, 110,411, 111,312, 113,619, 115,320, 117,122, 118,730, and 118,932. MRI specifications include: 3 Tesla (3T), 32-channel head coil, TR of 0.4 s, TE of 33 ms, FoV 208 mm in the read direction (anterior–posterior), 180 mm in the phase encoding direction, and 144 mm in the inferior–superior direction [43]. A multishell diffusion scheme was used, and the *b* values were 990, 1985, and 1980 s/mm^2. Each *b* value was sampled in 90 directions. The in-plane resolution was 1.25 mm. The slice thickness was 1.25 mm. The diffusion data were reconstructed using generalized q-sampling imaging with a diffusion sampling length ratio of 1.25 [54].

We performed brain registration to Montreal Neurologic Institute (MNI) space, wherein imaging is warped to fit a standardized brain model for comparison between subjects [4]. Tractography was performed in DSI Studio (Carnegie Mellon) using two predefined regions of interest (ROIs) to isolate single tracts. ROIs were traced to delineate the superior occipital, middle occipital, and inferior occipital gyri based upon the anatomic boundaries that we described earlier in this paper. Figure 2 demonstrates the ROIs that were defined as the superior, middle, and inferior occipital gyrus. Voxels within each ROI were automatically traced with randomized seeding of the voxel and/or tract with a maximum angular threshold of 45 degrees. When a voxel was approached with no tract direction or a direction change greater than 45 degrees, the tract was halted. Tractography was stopped after reaching a length of 450 mm, which is what we have

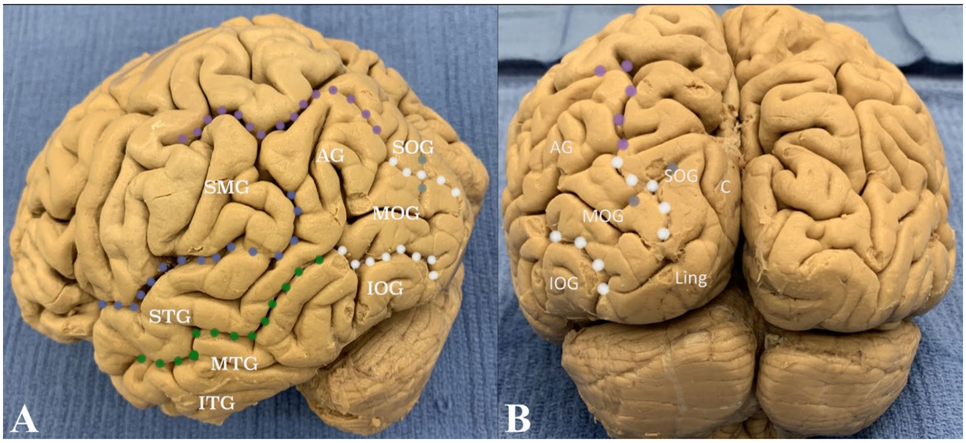

Fig. 1 The boundaries of the lateral occipital lobe demonstrated in panels **a** and **b**. The superior occipital gyrus is separated from the middle occipital gyrus by the intra-occipital sulcus (demarcated by the superior white dots). The middle occipital gyrus is bound by the intra-occipital sulcus and the lateral occipital sulcus (inferior white dots) and abuts the posterior portion of the angular gyrus. The inferior occipital gyrus is below the lateral occipital sulcus and abuts the posterior portion of the middle temporal gyrus. *SMG* supramarginal gyrus, *AG* angular gyrus, *SOG* superior occipital gyrus, *MOG* middle occipital gyrus, *IOG* inferior occipital gyrus, *STG* superior temporal gyrus, *MTG* middle temporal gyrus

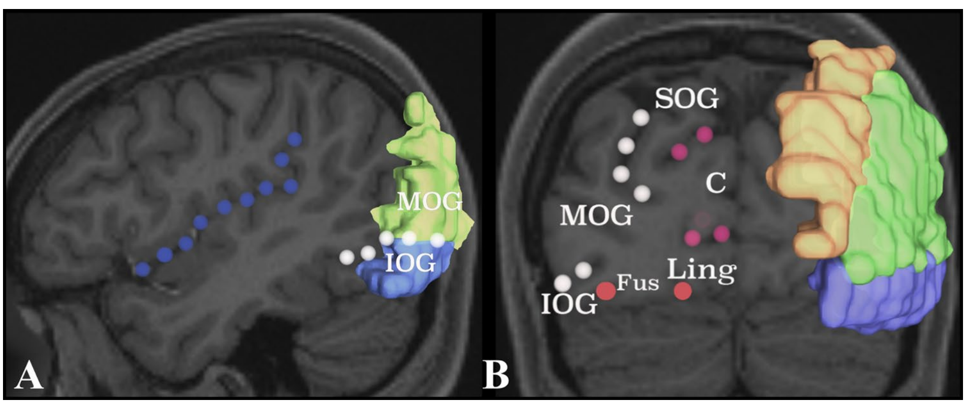

Fig. 2 The region of interest (ROI)s of the lateral occipital lobe. **a** A left-sided sagittal view, which demonstrates the lateral occipital sulcus (inferior white dots) which divided the inferior occipital gyrus and the middle occipital gyrus. **b** A coronal section of the brain, with the occipital lobe viewed from behind, which demonstrates the intra-occipital sulcus (superior white dots), which was used to delineate the middle occipital gyrus from the superior occipital gyrus. Notice the superior occipital gyrus continues all the way to the medial surface of the occipital lobe, where it becomes the cuneus. The lateral occipital sulcus (inferior white dots) separates the middle occipital gyrus. The inferior occipital gyrus ends at the basal surface of the occipital lobe, and is separated from the fusiform gyrus by the occipito-temporal sulcus (lateral red dot). For reference sake, the other gyri of the occipital lobe were demarcated. The fusiform gyrus was bound by the occipito-temporal sulcus (lateral red dot) and the collateral sulcus (medial red dot). The lingual gyrus was bound by the collateral sulcus and the calcarine sulcus (inferior magenta dots). The cuneus was bound inferiorly by the calcarine sulcus and superiorly by the parieto-occipital sulcus. The orange, green, and blue ROIs demarcate the superior, middle, and inferior occipital gyri, respectively. *SOG* superior occipital gyrus, *MOG* middle occipital gyrus, *IOG* inferior occipital gyrus, *C* cuneus, *Ling* lingual gyrus

used in other studies [5]. In some instances, exclusion ROIs were placed to remove spurious tracts not involved in the gyrus of interest. Fiber tractography was performed in both cerebral hemispheres for all regions of the lateral occipital cortex.

Lateralization indices

A lateralization index was calculated based on tract volumes for all major association fibers identified within the right and left cerebral hemispheres [46]. A Mann–Whitney *U* test was used to assess for any statistically significant differences in lateralization between tracts in the right and left cerebral hemispheres. All statistical analysis was performed with SPSS Version 22 (IBM Inc. New York, NY, USA).

Postmortem dissection

The purpose of the postmortem dissections was to demonstrate the location of major tracts connecting to the lateral occipital lobe. Postmortem dissections were performed using a modified Klingler technique [52]. Ten specimens were used for this study, obtained from our institution's Willed Body Program with approval of the state's anatomical board. The cadaveric brains were fixed in 10% formalin for at least 3 months after removal from the cranium. Up until the time of dissection, the pia-arachnoid membrane was left attached.

After fixation with formalin, specimens were rinsed with water for two days, and then frozen at − 10 °C for 8 h. After thawing, dissection of the specimens began with removal of the meninges and identification of cortical anatomy, including gyri and sulci. The brains were frozen to ease white matter dissections. When the water molecules freeze and expand within the white matter, the space is expanded allowing for easier dissection. The fibers are still connected and contiguous between their origin and termination so they are not disrupted. Relevant cortical areas were identified first. Starting superficially, they were then peeled back to reveal white matter areas of interest. Care was taken to leave cortical areas corresponding to white-tracts of interest intact in order to preserve their relationship. Tracts were dissected with blunt instruments to avoid disrupting the natural tract anatomy. Photographs were taken at each stage of the dissection.

Results

Long-range fibers

Middle longitudinal fasciculus

The lateral occipital lobe's main long-range fiber bundle is the middle longitudinal fasciculus (MdLF). Tractography demonstrated that the posterior end of the MdLF arises in the superior occipital gyrus and middle occipital gyrus. The fibers of the MdLF then join together and course antero-inferiorly through the inferior parietal lobule and Heschl's gyrus, lateral to the temporal horn of the lateral ventricle to terminate in the anterior and middle portions of the superior temporal gyrus. These fibers are demonstrated in Fig. 3a–c. This dissection was started by exposing the superior and middle occipital gyrus and locating white matter fibers that extended from there to the inferior parietal lobule. Once these were detected, the dissection was continued into the superior temporal gyrus. Once this portion of the MdLF was dissected, the contributions of this white matter pathway from the precuneus (parietal lobe) and cuneus (occipital lobe) were also exposed (Fig. 3d).

Inferior longitudinal fasciculus

Another main long-range fiber of the lateral occipital lobe is the inferior longitudinal fasciculus. Tractography determined that the posterior end of the ILF arises in the inferior occipital gyrus, demarcated as being located underneath the lateral occipital sulcus. Our tractography also demonstrates that it had its anterior end in the temporal pole, primarily at the inferior temporal gyrus.

During our dissection, we dissected around the lateral occipital sulcus to reveal the posterior end of the ILF in the gray matter of the inferior occipital gyrus. We then followed it as it coursed underneath the lateral occipital sulcus, into the white matter of the occipital lobe, remaining lateral of the temporal horn of the lateral ventricle. It then headed anteriorly to the temporal pole to end at the inferior temporal gyrus. We then headed back to the deep white matter of the occipital lobe, and dissected posteriorly to expose the contributions of the ILF from the cuneus and the lingual gyrus. Tractography is demonstrated in Fig. 4a with the dissection demonstrated in 4b. We wanted to focus on the deep white matter of the occipital lobe in Fig. 4c, to demonstrate how to dissect fibers of the ILF back to the medial occipital lobe.

Inferior Fronto-Occipital Fasciculus

A small subcomponent of the inferior fronto-occipital fasciculus was found in the lateral occipital lobe. Wu et al. had demonstrated five subcomponents of the IFOF, in which he described some subcomponents as having terminations in the lateral occipital lobe. In tractography, we demonstrated that these fibers were present. The posterior end was positioned at the infero-lateral portion of the inferior occipital gyrus. From there, we were able to see them course through the deep white matter of the occipital lobe, remaining lateral to the horn of the ventricle. They remained lateral to the temporal horn as they coursed through the temporal lobe, until turning medially into the anterior potion of the short gyri of the insula. Their anterior termination was located primarily in the orbitofrontal cortex. We confirmed this through dissection by exposing the IFOF connections at the cuneus and lingual gyrus. After performing this deep dissection, we slowly extended the posterior dissection to include the lateral occipital lobe, which revealed that fibers of the IFOF had a contribution from the lateral occipital lobe. We then continued to dissect fibers of the deep white matter which led us to the medial occipital lobe (lingual gyrus and cuneus); these

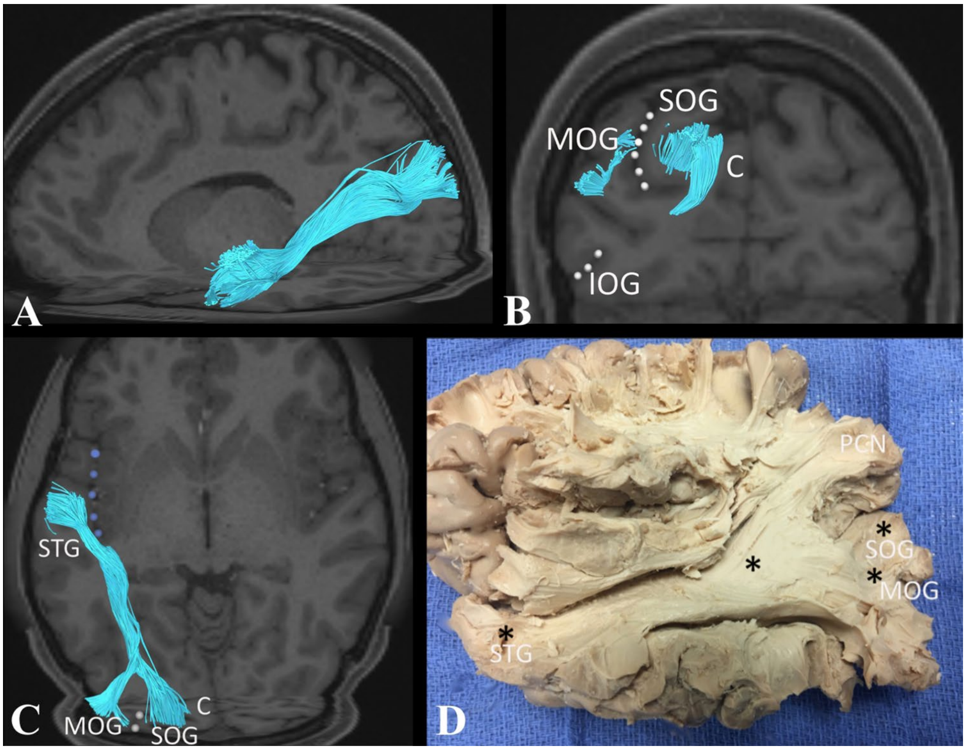

Fig. 3 The MdLF connection from the superior occipital gyrus to the superior temporal gyrus. **a** A sagittal section, demonstrating these connections. **b** A coronal section, with a view from behind, which demonstrates subcomponents of the MdLF in the middle and superior occipital gyrus. Notice the clear demarcation of the superior and middle occipital gyrus at the intra-occipital sulcus (superior white dots). **c** Its anterior termination in the superior temporal gyrus. **d** The posterior terminations of the MdLF in the superior and middle occipital gyri, which meet together and course through the inferior parietal lobule, and then has posterior terminations in the superior temporal gyrus (course demarcated by black stars). We also included the contribution of the precuneus (parietal lobe) to the MdLF. *C* cuneus, *SOG* superior occipital gyrus, *MOG* middle occipital gyrus, *IOG* inferior occipital gyrus, *PCN* precuneus, *STG* superior temporal gyrus

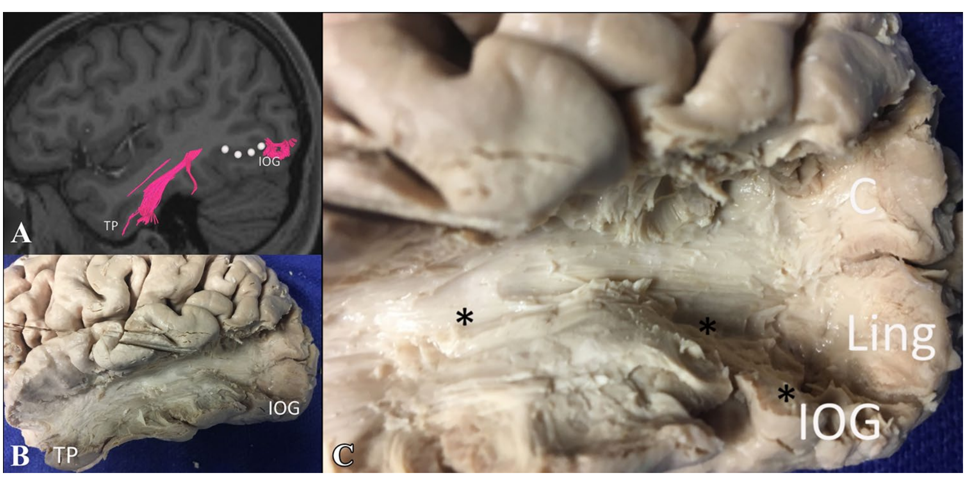

Fig. 4 The ILF connection from the inferior occipital gyrus to the inferior temporal gyrus at the temporal pole. **a** Fibers from the inferior occipital gyrus, demarcated inferior to the lateral occipital sulcus (white dots) coursing to the inferior temporal gyrus on tractography. **b** A dissection that was performed of the ILF, confirming its anterior and posterior terminations. When focusing on the deep white matter of the occipital lobe, as seen in **c**, we can see that fibers from the inferior occipital gyrus course underneath the lateral occipital sulcus (black stars) and join ILF subcomponents from the cuneus and lingual gyrus to make the complete white matter tract. *IOG* inferior occipital gyrus, *TP* temporal pole, *C* cuneus, *Ling* lingual gyrus

fibers mainly have their anterior termination in the superior frontal gyrus. There are reports of these terminations within the medial occipital lobe [39, 50]. Tractography can be seen in Fig. 5 along with our dissection.

Intra-occipital fibers

Fibers were also detected between the superior occipital gyrus, cuneus and the inferior occipital gyrus, with extension into the fusiform. The morphology of this tract is consistent with the vertical occipital fasciculus (VOF). Tractography demonstrated that the superior end of the VOF present primarily in the superior occipital gyrus extending medially into the cuneus. As shown by the dissection, these fibers extend to the posterior portion of the angular gyrus, though this was not the focus of our dissection. The fibers then course inferiorly and have one set of fibers course to the inferior occipital gyrus (underneath the lateral occipital sulcus) and another set of fibers course inferiorly at about a forty-five degree angle to have an end in the fusiform gyrus. Our dissection started by identifying the intra-parietal sulcus, following it posteriorly to the intra-occipital sulcus (continuation of the intra-parietal sulcus past the parieto-occipital sulcus). The intra-occipital sulcus divided the superior and middle occipital gyrus. We dissected around this area to expose the superior end of the VOF at the superior occipital gyrus. We followed its course through the deep white matter adjacent to the medial occipital gyrus. We remained lateral to the occipital horn of the lateral ventricle. We then dissected the area around the lateral occipital sulcus to expose the inferior end of the VOF at the inferior occipital gyrus and another set at the fusiform gyrus. Our tractography along with dissection are demonstrated in Fig. 6.

Intra-occipital connections were also detected between the inferior occipital gyrus and the fusiform gyrus. Tractography demonstrates that the posterior end of the fibers arise within the lateral portion of the inferior occipital gyrus. They then course over the occipito-temporal gyrus and the anterior end of the fibers at the anterior portion of the fusiform gyrus. We confirmed this in dissection by dissecting the area around the occipito-temporal sulcus. Once the gray matter was cored in that area we discovered the tract's posterior end in the inferior occipital gyrus and then followed it anteriorly to the fusiform gyrus. These fibers can be seen in Fig. 7.

Parietal connections to the lateral occipital lobe

U-shaped association fibers were also seen connecting gyri adjacent to the lateral occipital lobe. Tractography detected fibers with a posterior ending in middle occipital gyrus coursing anteriorly through the deep white matter of the angular gyrus, which abuts the middle occipital gyrus, before reaching its anterior end in the superior parietal lobule. These fibers were detected by starting the dissection at the intra-parietal sulcus (dividing the superior parietal lobule and the inferior parietal lobule). It was used to reveal the anterior end at the superior parietal lobule. The intra-parietal sulcus was followed until reaching the intra-occipital sulcus, which divides the superior occipital gyrus and the middle occipital gyrus. We followed these fibers from the superior parietal lobule, coursing through

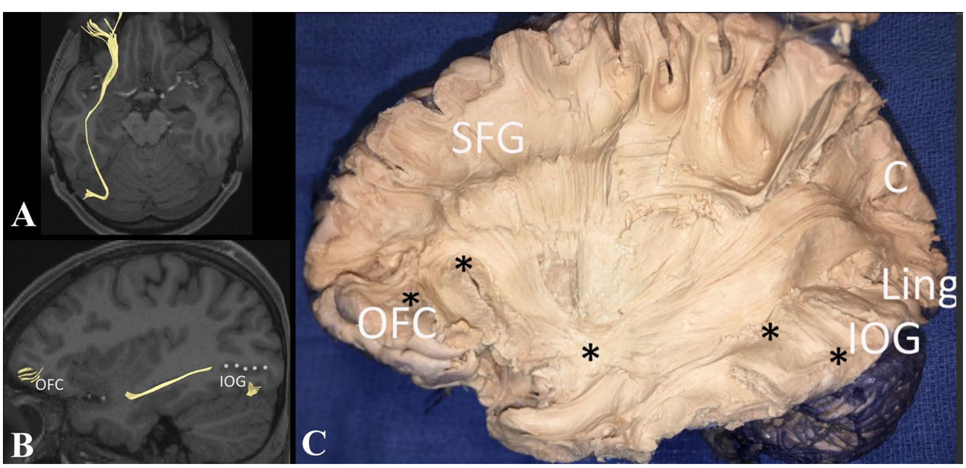

Fig. 5 The IFOF is dissected. Tractography confirmed its course from the occipital lobe to the frontal lobe. In **a**, we see a horizontal section showing connections between the frontal and occipital lobes. In **b**, we see that the IFOF has subcomponents in the inferior occipital gyrus, demarcated inferior to the lateral occipital sulcus (white dots), with an anterior termination in the orbitofrontal cortex. We started our dissection in **c** by exposing the other subcomponents of the IFOF in the medial occipital lobe (lingual gyrus and cuneus) which reach the superior frontal gyrus and extending this dissection laterally and inferiorly to include the subcomponent of interest (in black dots). *OFC* orbitofrontal cortex, *SFG* superior frontal gyrus, *IOG* inferior occipital gyrus, *Ling* lingual gyrus, *C* cuneus

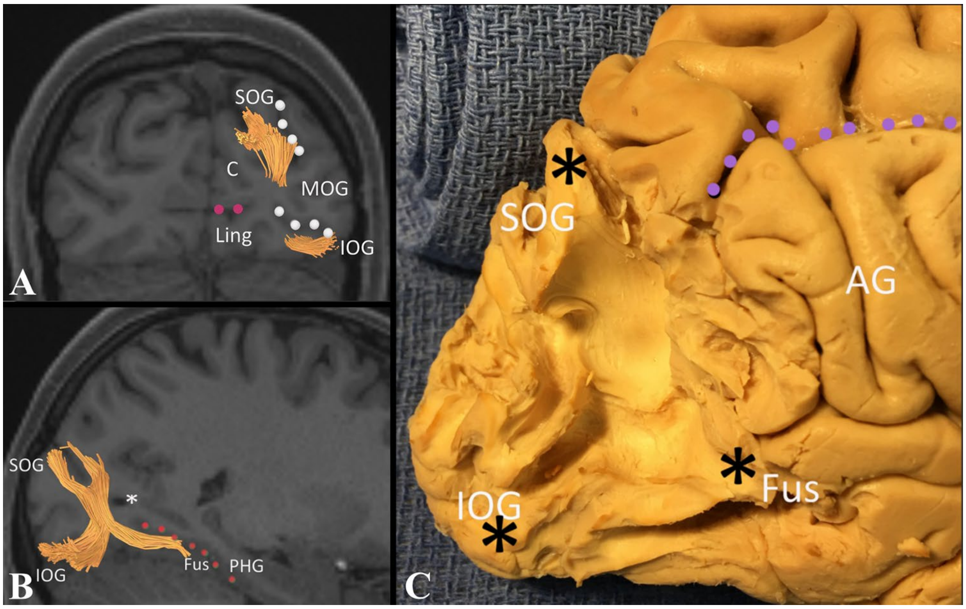

Fig. 6 The full extent of the VOF is demonstrated. **a** A coronal section, viewed from the back, which demonstrates a subcomponent of the VOF that has its superior terminations in the superior occipital gyrus and cuneus and inferior terminations in the inferior occipital gyrus. The intra-occipital sulcus (superior white dots) and lateral occipital sulcus (inferior white dots) separate the superior and middle along with the middle and inferior occipital gyri, respectively. **b** Is a right-sided sagittal section, which demonstrates another subcomponent of the VOF from the superior occipital gyrus that reaches the fusiform gyrus (red dots demarcate the collateral sulcus medially). Notice how these fibers remain lateral to the occipital horn of the lateral ventricle. In **c**, we started our dissection by following the intraparietal sulcus (purple dots) to the intra-occipital sulcus. We use it to find the superior occipital gyrus and follow its fibers that coursed downwards to the inferior occipital gyrus and fusiform gyrus (black dots). *SOG* superior occipital gyrus, *Fus* fusiform gyrus, *IOG* inferior occipital gyrus, *AG* angular gyrus

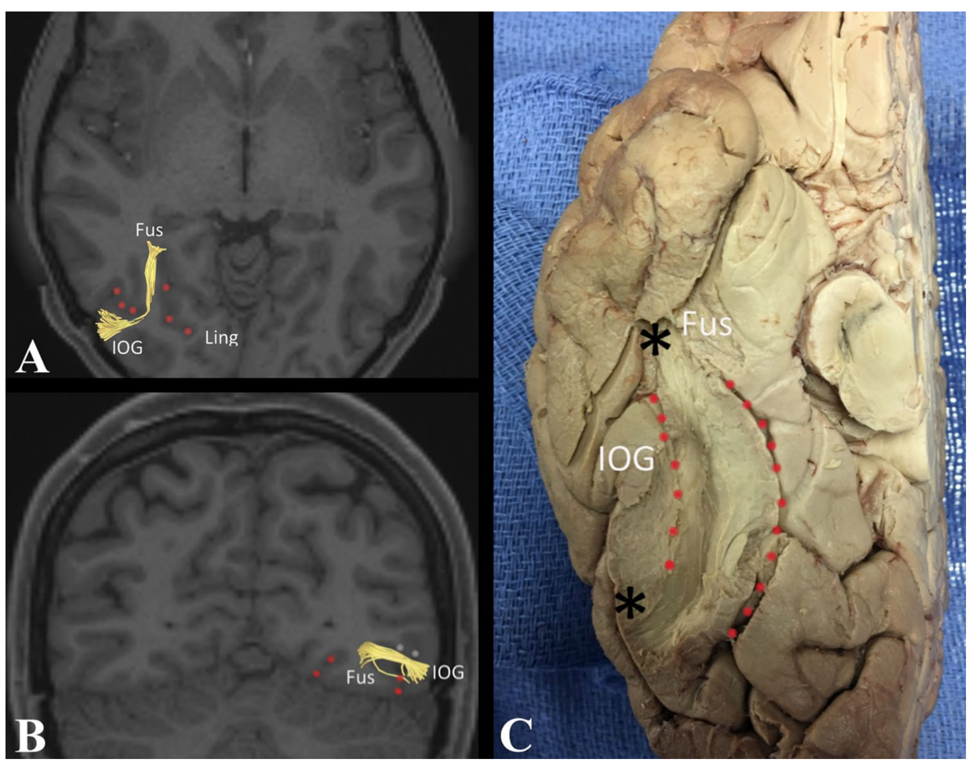

Fig. 7 The connection between the inferior occipital gyrus and the fusiform gyrus demonstrated in tractography. **a** An axial section is demonstrated, looking from bottom-up (same orientation as dissection figure), with posterior terminations in the inferior occipital gyrus and anterior termination in the fusiform gyrus. **b** A coronal section, viewed from behind, which demonstrates its course over the occipito-temporal sulcus (lateral red dots). **c** The occipito-temporal sulcus (lateral red dots) cored to demonstrate fibers from the inferior occipital gyrus to the fusiform gyrus (black dots). *IOG* inferior occipital gyrus, *Fus* fusiform gyrus

the deep white matter of the angular gyrus, then ending at the middle occipital gyrus. The tractography and the dissection can be visualized in Fig. 8.

U-shaped fibers

When beginning cadaveric dissection, short fiber bundles between adjacent gyri were observed immediately beneath the cortical surface of the occipital lobe. These short association fibers are commonly referred to as U-shaped fibers, given their characteristic morphology. One example of U-shaped fibers is the fiber bundle originating in the inferior portion of the superior occipital gyrus and terminating within the middle occipital gyrus after traversing the transverse occipital sulcus. An example of this U-fiber is demonstrated in Fig. 9. A similar series of U-shape fibers was seen between the middle occipital gyrus and inferior occipital gyrus as well as superior occipital gyrus and medial occipital cortex of the cuneus. The diverse array of U-shaped fibers shown in Fig. 10 highlights the interconnectedness of the lateral occipital lobe to adjacent cortical areas.

Relationship of white matter fibers within the occipital lobe

The major white matter fibers were studied in relation to the optic tracts, a system that feeds visual information into the occipital lobe [40]. The optic radiations have their anterior end originating in the lateral geniculate nucleus of the thalamus. These fibers then head posteriorly, remaining lateral to the atrium of the ventricle, and have their posterior end along the superior occipital gyrus, cuneus, and the lingual gyrus. Our dissection confirmed this presence by first dissecting out the anterior end at the lateral geniculate nucleus. We then followed these fibers around the lateral portion of the atrium, following them back through the occipital lobe. This can be seen in Fig. 11.

Using GQI-based tractography, we looked to study the relationship of the optic radiations to the MdLF, VOF, IFOF, and ILF. The fibers of the MdLF, VOF, and optic radiations interdigitate within the superior occipital gyrus as seen in the Fig. 12a, b. The VOF had one connection from the superior occipital gyrus that reached the inferior occipital gyrus. In the inferior occipital gyrus, fibers of the VOF interdigitate with the IFOF and ILF. In Fig. 12c, we demonstrated that all

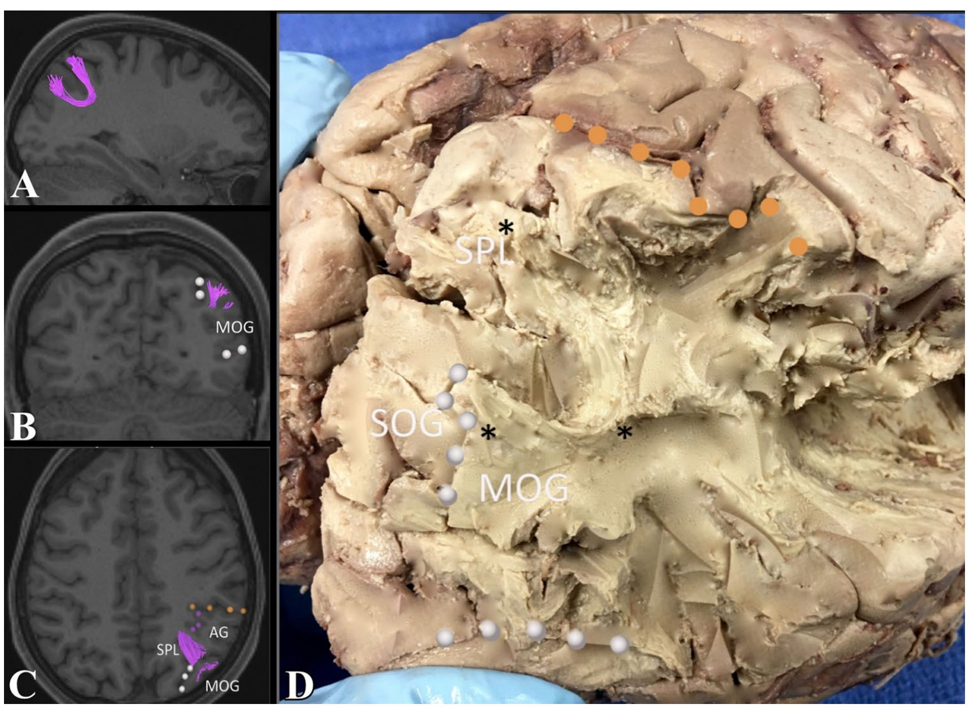

Fig. 8 The white matter fibers connecting the middle occipital gyrus to the superior parietal lobule. **a** A sagittal section demonstrating this connection. **b** A coronal section when viewed from behind, demonstrated the posterior terminations in the middle occipital gyrus. This was bound by the intra-occipital sulcus (superior white dots) and the lateral occipital sulcus (inferior white dots). **c** An axial section in which the anterior termination can be seen in the superior parietal lobule. The superior parietal lobule is located above the intra-parietal sulcus (shown in purple dots). **d** The dissection. We started at the intra-occipital sulcus and found the posterior terminations in the middle occipital gyrus. It was followed through the angular gyrus until reaching the superior parietal lobule. *SOG* superior occipital gyrus, *MOG* middle occipital gyrus, *AG* angular gyrus, *SPL* superior parietal lobule

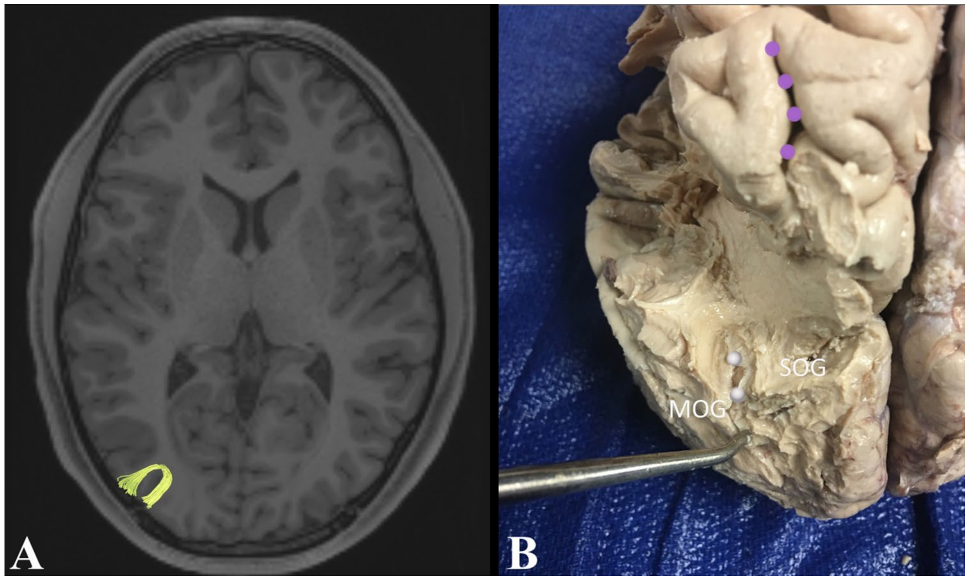

Fig. 9 **a** U-shaped fiber that was detected between the superior and middle occipital gyrus in tractography. It was confirmed through dissection in **b**. *SOG* superior occipital gyrus, *MOG* middle occipital gyrus

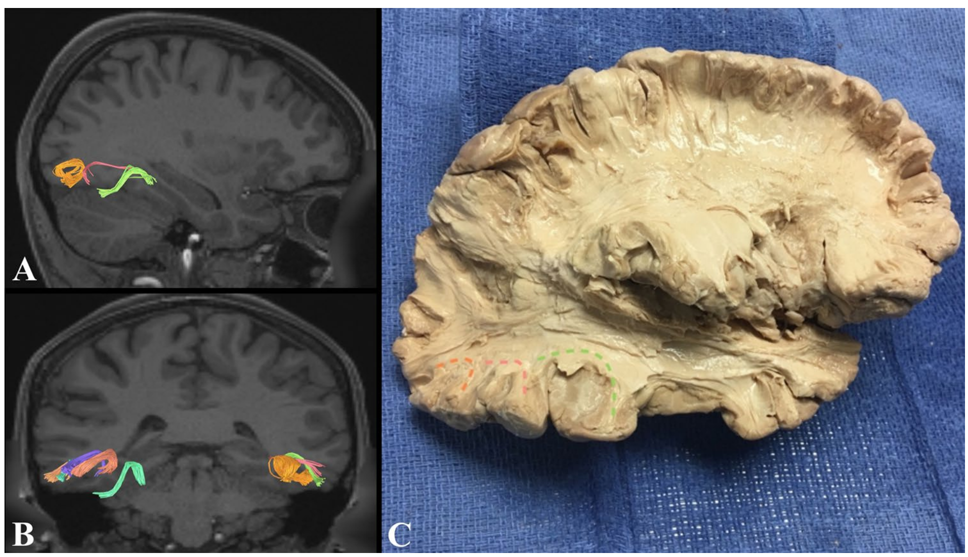

Fig. 10 Dissections demonstrated most of the U fibers in the lateral occipital cortex (**a**, **b**), which were confirmed in tractography

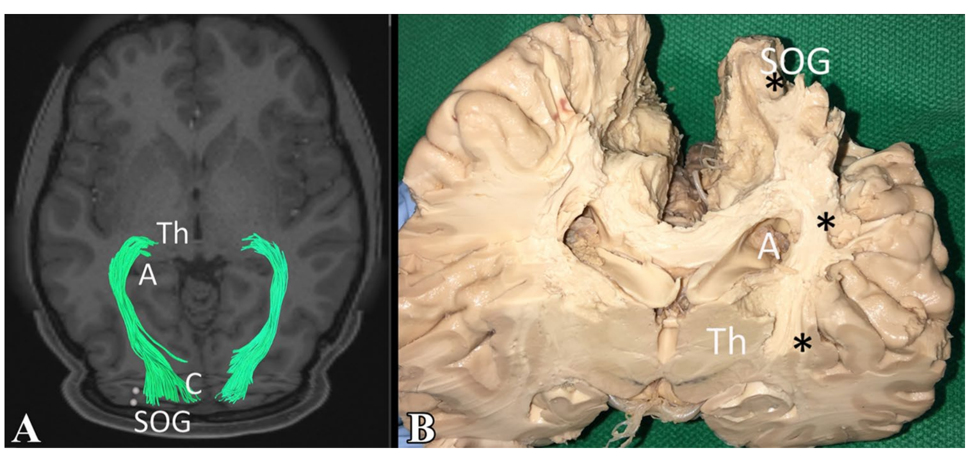

Fig. 11 **a** The optic radiations. Fibers from the lateral geniculate nucleus of the thalamus wrap laterally around the atrium. They course posteriorly and spread across the superior occipital gyrus, cuneus, and lingual gyrus. **b** A dissected portion of the optic radiations that reach the superior occipital gyrus from the lateral geniculate nucleus (black stars). *SOG* superior occipital gyrus, *A* atrium, *Th* thalamus, *C* cuneus

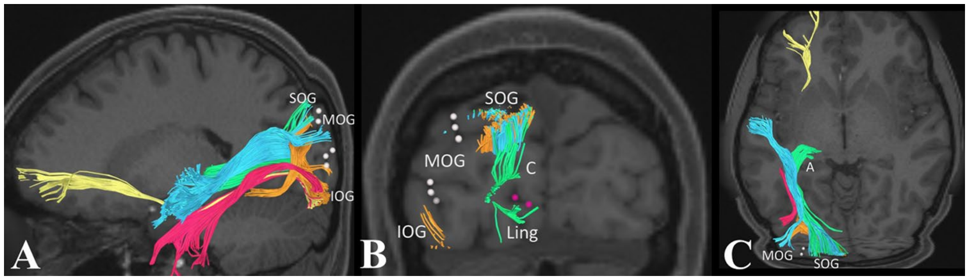

Fig. 12 The relationship of the optic radiations to the IFOF (yellow), ILF (magenta), MdLF (blue), and VOF (orange). **a** A sagittal section demonstrating these tracts. **b** A coronal section when viewed from behind demonstrates the interdigitation of fibers of the MdLF, optic radiations, and VOF at the superior occipital gyrus. **c** How these fibers remain lateral to the ventricle as they reach their anterior terminations. *SOG* superior occipital gyrus, *MOG* middle occipital gyrus, *IOG* inferior occipital gyrus, *C* cuneus, *Ling* lingual gyrus (color figure online)

these long-range fibers all remained lateral to the temporal horn, atrium, and occipital horn.

Lateralization indices

We calculated lateralization indices based on tract volumes for the right and left VOF and MdLF across all ten tractography subjects included in this analysis. No significant differences in the lateralization index were detected between the right and left MdLF ($p=0.52$), or the right and left VOF ($p=0.95$). Other reports have demonstrated prominent lateralization of tracts such as the ILF and MdLF [35, 39]. There were no significant differences in the lateralization index with the fibers that coursed through the inferior occipital gyrus and the fusiform gyrus.

Discussion

In this study, we describe the underlying white matter anatomy of the lateral occipital lobe. The view that functional preservation in cerebral surgery is dependent on preserving connections between components of functional networks has become broadly accepted [14]. Using diffusion spectrum tractography confirmed by gross anatomic dissection, we describe the connections of the lateral occipital cortex in ten normal subjects and ten cerebral hemispheres, respectively. We found good concordance between the methodologies employed in this study.

Relation of tractography to gross dissection

Middle longitudinal fasciculus (MdLF)

The MdLF has been described previously in the literature. However, different studies have proposed different cortical endpoints for this white matter tract. For example, several studies have proposed that the MdLF extends from the anterior superior temporal gyrus to the angular gyrus [30, 33]. Discovery of cortical terminations of the MdLF within the human angular gyrus is consistent with other studies in non-human primates [42]. However, given the limitations of GQI-based fiber tractography, the authors concluded that the MdLF may extend into the occipital lobe [33]. Additional studies have described such projections of the MdLF from the superior temporal gyrus into the precuneus and occipital lobe [31, 33, 49]. Our dissections are consistent with these findings, as we describe a component of the MdLF terminating in the superior occipital gyrus of the lateral occipital cortex. Fibers were also found continuing into the medial occipital lobe to the cuneus and additionally to the precuneus. One of the limits of GQI-based fiber tractography is that this imaging modality assumes that there is a unique orientation of fibers, with a direction that is defined by the tensor's eigenvector. However, in cases where there are fibers that are interdigitating, GQI-based fiber tractography cannot locate these fibers at times. With the MdLF having fibers that cross the VOF and U-shape fibers, as demonstrated in Fig. 13, we understand why prior studies have not been able to locate it in the superior occipital gyrus.

Based on its terminations in the angular gyrus, some have ascribed a role for the MdLF in language processing [33]. However, intraoperative electrostimulation of the MdLF does not disrupt an individual's ability to complete picture-naming tasks [13]. Similarly, no post-operative language deficits were discovered in the same cohort of patients after resecting extensive portions of the MdLF [13]. Others have suggested that the MdLF represents a dorsal auditory pathway integrated within functional areas of the dorsal visual stream to assist in the spatial localization of sound [49]. Integration of audio and visual inputs for the purposes of object recognition has also been linked to the lateral occipital lobe [15]. The MdLF may play a role in this integration within the lateral occipital cortex.

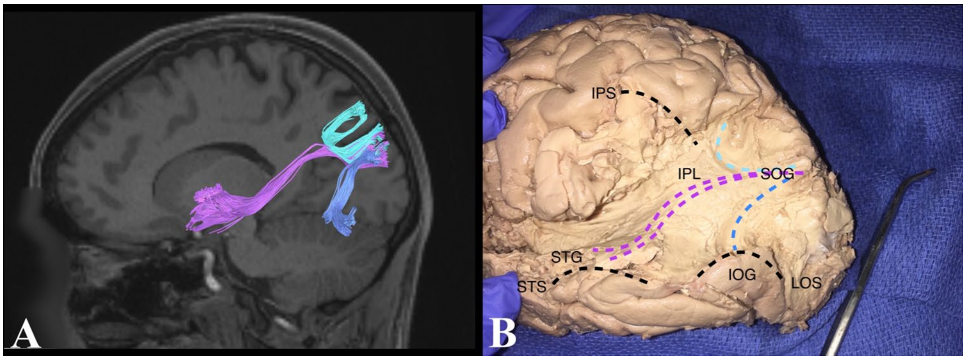

Fig. 13 The fibers of the MdLF interdigitating with fibers of the VOF and fibers of the superior occipital gyrus and posterior parietal cortex. Figure 8**a** demonstrates the tractography while **b** demonstrates the confirmed dissection. *IPS* intra-parietal sulcus, *IPL* inferior parietal lobule, *STS* superior temporal sulcus, *STG* superior temporal gyrus, *LOS* lateral occipital sulcus, *IOG* inferior occipital gyrus, *SOG* superior occipital gyrus

Vertical occipital fasciculus (VOF)

The vertical occipital fasciculus was originally discovered by Wernicke through dissection in monkeys (1881) and was subsequently identified in human studies by Obersteiner (1888) [53]. The VOF has been cited as having one end in the inferior occipital and fusiform gyri, extending to the superior occipital gyrus, cuneus, and angular gyrus [51, 53]. Our dissections show that the VOF projects from the superior occipital gyrus to the inferior occipital gyrus, with extension into areas of both the dorsal stream, including the cuneus and posterior angular gyrus, and ventral stream, including the basal occipital lobe and fusiform gyrus.

Given its anatomic connections, several studies have focused on the functional role of the VOF in linking the dorsal and ventral visual streams. For example, the posterior portion of the VOF has been shown to play a role in communicating spatial information between cortical regions of the two streams [53]. Additional studies have shown that areas connected to the VOF in the ventral stream (such as ventromedial visual area 1(VMV1), ventromedial visual area 2 (VMV2), and ventromedial visual area 3 (VMV3)) are important for integrating color, texture, and form. Similarly, areas connected to the VOF in the dorsal stream (such as V3a) are important for integrating spatial information [6, 10]. The VOF has also been linked in the stereoscopic depth perception of objects [38].

c. Inferior Occipito-Frontal Fasciculus and Inferior Longitudinal Fasciculus.

The inferior occipito-frontal fasciculus and the inferior longitudinal fasciculus were identified to have subcomponents with their posterior terminations in the inferior occipital gyrus. Our data supported the work of Wu et al. and Panesar et al., who described subcomponents of the IFOF and the ILF in the inferior occipital gyrus [39, 51]. The subcomponent fibers of the IFOF and the ILF in the inferior occipital gyrus were shown to interdigitate with the VOF.

Functional networks of the lateral occipital cortex

The lateral occipital lobe is heavily interconnected via U-shaped fibers to adjacent parts of the cortex, including the posterior parietal cortex and the fusiform gyrus. Figure 14 demonstrates all tracts that were reported and demonstrates this interconnected network. We can see that it contains fibers associated with the dorsal stream (U-shaped fibers) and the "dorsal auditory pathway" (MdLF). We can also see fibers associated with the ventral stream the IFOF, ILF, and successive U-shaped fibers. These fibers are interconnected by the VOF. We also observe heavy connections with adjacent gyri, such as the fusiform gyrus. Together these findings suggest that higher order functions occurring within the lateral occipital cortex, such as object recognition, facial

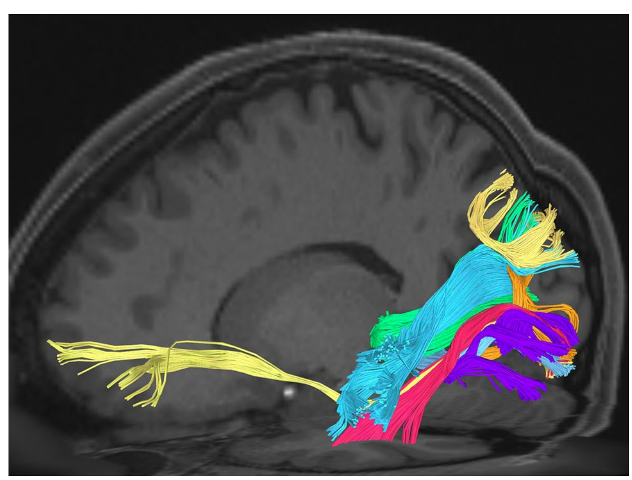

Fig. 14 The tracts of the lateral occipital lobe demonstrated

recognition, and motion perception are likely related to the intricate local fiber bundles described in this study [32, 36, 47].

The lateral occipital cortex and object recognition

The lateral occipital cortex is a well-known processing center for object recognition [16, 19, 23, 32, 37, 44, 45]. Functional magnetic resonance imaging (fMRI) studies demonstrate that the lateral occipital cortex preferentially activates in response to pictures of objects, regardless of image features or familiarity [32]. Others have demonstrated that light, contrast, motion, and texture can activate the lateral occipital cortex if they contribute to object form [19]. Additional fMRI studies have shown that the lateral occipital cortex activates when individuals detect object silhouettes [26]. The lateral occipital cortex may be thought of as a terminal processing center of the ventral visual stream, uniting disparate information such as shape, form, and orientation to perceive an object's physical representation in space [34].

Beyond the visual perception of objects, the lateral occipital cortex shows activity during haptic-related sensory activation [24, 44]. Because of this, some argue that the lateral occipital cortex represents a multi-modal object recognition network [2, 3], responsive to the visual, auditory, and tactile senses [2, 27]. In addition, transcranial magnetic stimulation of the lateral occipital cortex is associated with worsening performance on audio-visual object recognition tasks [15].

The lateral occipital lobe and facial recognition

The lateral occipital cortex is also involved in facial recognition [21, 36]. This part of the brain is associated with higher levels of functional activity when individuals examine faces as opposed to cars [29]. This has led some to hypothesize that facial recognition and object recognition involve distinct sets of neurons in the brain, i.e., that both object and face-selective neurons exist [20]. Fiber tractography and gross dissection revealed a connection between the inferior occipital gyrus and an area of the fusiform gyrus known as the fusiform face area (FFA) [25]. The fusiform face area receives information about invariant facial features from the lateral occipital lobe to produce a complete facial form [9]. The connection between the inferior occipital gyrus and the fusiform gyrus described in this study suggests one subcortical pathway by which this information transfer may occur.

The lateral occipital lobe and motion perception

The lateral occipital lobe is also involved in motion perception. Positron emission tomography studies have shown that area MT in the lateral occipital lobe responds to visual motion [47]. This region is located in the lateral occipital sulcus, inferior to the angular gyrus. Similarly, MST, a distinct area in the human MT complex, demonstrates preferential activation when objects rotate [48]. MST has also been shown to play a role in the integration, analysis, and perception of visual motion [11].

The middle longitudinal fasciculus, vertical occipital fasciculus, and a diverse array of U-shaped fibers connect the lateral occipital lobe to parts of the temporal, parietal, and medial occipital cortices. The complex functional processes attributed to the lateral occipital lobe, including object recognition, facial recognition, and motion perception are likely related to the subcortical white matter tracts described within this study.

Limitations

One of the main limitations of this paper is the fact that the 10 brains that were dissected were different from the 10 brains that were used for tractography. As we are not able to perform DTI-based imaging on the cadavers that were used, we chose to use imaging provided by the Human Connectome project. Furthermore, we were not able to determine the age and sex of the cadaveric brains that were used, which prevents us from comparing them to subjects that were used for tractography.

Additionally, we did not perform any functional studies to determine what functional roles these white matter tracts held. We have identified fibers which we believe are associated with the dorsal and ventral stream. Additionally, we demonstrated fibers that have a close association with both visual streams. This complex makeup of fibers allows for visual information to be detected, and for perceptual processing of discrete details and whole images. Furthermore, this information must be relayed to various regions of the brain responsible for attentional, spatial, and semantic integration. Our study is not meant to determine which fibers should be attributed to these functions. Instead, we aim to demonstrate the white matter anatomy of the lateral occipital lobe, which has complex interactions giving rise to its attributed functions.

Lastly, we generated white matter tracts using deterministic tractography instead of probabilistic tractography. Currently, the field of neurosurgery uses deterministic tractography for surgical planning due to its reproducibility. The authors would like to note that probabilistic tractography would be more accurate regarding cross-fiber generation; however, the tracts described in this report are generally well accepted and known to have the described cortical connections and anatomic locations.

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References

1. Alves RV, Ribas GC, Parraga RG et al (2012) The occipital lobe convexity sulci and gyri. J Neurosurg 116:1014–1023
2. Amedi A, Jacobson G, Hendler T et al (2002) Convergence of visual and tactile shape processing in the human lateral occipital complex. Cereb Cortex 12:1202–1212
3. Amedi A, Malach R, Hendler T et al (2001) Visuo-haptic object-related activation in the ventral visual pathway. Nat Neurosci 4:324
4. Ardekani BA, Tabesh A, Sevy S et al (2011) Diffusion tensor imaging reliably differentiates patients with schizophrenia from healthy volunteers. Hum Brain Mapp 32:1–9
5. Baker CM, Burks JD, Briggs RG et al (2018) A connectomic atlas of the human cerebrum-chapter 1: introduction, methods, and significance. Oper Neurosurg 15:1–9
6. Baker CM, Burks JD, Briggs RG et al (2018) A connectomic atlas of the human cerebrum-chapter 9: the occipital lobe. Oper Neurosurg (Hagerstown) 15:372–406
7. Bankson BB, Hebart MN, Groen IIA et al (2018) The temporal evolution of conceptual object representations revealed through models of behavior, semantics and deep neural networks. Neuroimage 178:172–182
8. Bernard F, Lemée J-M, Ter Minassian A et al (2018) Right hemisphere cognitive functions: from clinical and anatomic bases to brain mapping during awake craniotomy part i: clinical and functional anatomy. World Neurosurg 118:348–359
9. Bernstein M, Erez Y, Blank I et al (2018) An integrated neural framework for dynamic and static face processing. Sci Rep 8:7036
10. Briggs RG, Conner AK, Sali G et al (2018) A connectomic atlas of the human cerebrum-chapter 16: tractographic description of the vertical occipital fasciculus. Oper Neurosurg (Hagerstown) 15:456–461
11. Britten KH, Heuer HW (1999) Spatial summation in the receptive fields of MT neurons. J Neurosci 19:5074–5084
12. Budisavljevic S, Dell'acqua F, Castiello U (2018) Cross-talk connections underlying dorsal and ventral stream integration during hand actions. Cortex 103:224–239
13. De Witt Hamer PC, Moritz-Gasser S, Gatignol P et al (2011) Is the human left middle longitudinal fascicle essential for language? A brain electrostimulation study. Hum Brain Mapp 32:962–973
14. Duffau H (2012) The challenge to remove diffuse low-grade gliomas while preserving brain functions. Acta Neurochir (Wien) 154:569–574
15. Giovannelli F, Giganti F, Righi S et al (2016) Audio-visual integration effect in lateral occipital cortex during an object recognition task: an interference pilot study. Brain Stimul 9:574–576
16. Goebel R, Muckli L, Zanella FE et al (2001) Sustained extrastriate cortical activation without visual awareness revealed by fMRI studies of hemianopic patients. Vision Res 41:1459–1474
17. Goodale MA, Milner AD (1992) Separate visual pathways for perception and action. Trends Neurosci 15:20–25
18. Goodale MA, Milner AD (2018) Two visual pathways where have they taken us and where will they lead in future? Cortex 98:283–292
19. Grill-Spector K, Kourtzi Z, Kanwisher N (2001) The lateral occipital complex and its role in object recognition. Vision Res 41:1409–1422
20. Grill-Spector K, Kushnir T, Edelman S et al (1999) Differential processing of objects under various viewing conditions in the human lateral occipital complex. Neuron 24:187–203
21. Haxby JV, Grady CL, Horwitz B et al (1991) Dissociation of object and spatial visual processing pathways in human extrastriate cortex. Proc Natl Acad Sci 88:1621
22. Hebart MN, Hesselmann G (2012) What visual information is processed in the human dorsal stream? J Neurosci 32:8107–8109
23. James TW, Culham J, Humphrey GK et al (2003) Ventral occipital lesions impair object recognition but not object-directed grasping: an fMRI study. Brain 126:2463–2475
24. James TW, Humphrey GK, Gati JS et al (2002) Haptic study of three-dimensional objects activates extrastriate visual areas. Neuropsychologia 40:1706–1714
25. Kanwisher N, Mcdermott J, Chun MM (1997) The fusiform face area: a module in human extrastriate cortex specialized for face perception. J Neurosci 17:4302–4311
26. Kourtzi Z, Erb M, Grodd W et al (2003) Representation of the perceived 3-D object shape in the human lateral occipital complex. Cerebral Cortex 13:911–920
27. Lacey S, Sathian K (2014) Visuo-haptic multisensory object recognition, categorization, and representation. Front Psychol 5:730
28. Lemee JM, Bernard F, Ter Minassian A et al (2018) Right Hemisphere Cognitive Functions: from Clinical and Anatomical Bases to Brain Mapping During Awake Craniotomy. Part II: Neuropsychological Tasks and Brain Mapping. World Neurosurg 118:360–367
29. Lerner Y, Hendler T, Ben-Bashat D et al (2001) A Hierarchical Axis of Object Processing Stages in the Human Visual Cortex. Cereb Cortex 11:287–297
30. Makris N, Preti MG, Asami T et al (2013) Human middle longitudinal fascicle: variations in patterns of anatomical connections. Brain Struct Funct 218:951–968
31. Makris N, Preti MG, Wassermann D et al (2013) Human middle longitudinal fascicle: segregation and behavioral-clinical implications of two distinct fiber connections linking temporal pole and superior temporal gyrus with the angular gyrus or superior parietal lobule using multi-tensor tractography. Brain Imaging Behav 7:335–352
32. Malach R, Reppas JB, Benson RR et al (1995) Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. Proc Natl Acad Sci USA 92:8135–8139
33. Maldonado IL, De Champfleur NM, Velut S et al (2013) Evidence of a middle longitudinal fasciculus in the human brain from fiber dissection. J Anat 223:38–45
34. Margalit E, Shah MP, Tjan BS et al (2016) The Lateral Occipital Complex shows no net response to object familiarity. J Vis 16:3–3
35. Menjot De Champfleur N, Lima Maldonado I, Moritz-Gasser S et al (2013) Middle longitudinal fasciculus delineation within language pathways: a diffusion tensor imaging study in human. Eur J Radiol 82:151–157
36. Nagy K, Greenlee M, Kovács G (2012) The lateral occipital cortex in the face perception network: an effective connectivity study. Front Psychol. https://doi.org/10.3389/fpsyg.2012.00141
37. Niemeier M, Goltz HC, Kuchinad A et al (2005) A Contralateral Preference in the Lateral Occipital Area: sensory and Attentional Mechanisms. Cereb Cortex 15:325–331
38. Oishi H, Takemura H, Aoki SC et al (2018) Microstructural properties of the vertical occipital fasciculus explain the variability in human stereoacuity. Proc Natl Acad Sci USA 115:12289–12294
39. Panesar SS, Yeh FC, Jacquesson T et al (2018) A Quantitative Tractography Study Into the Connectivity, Segmentation and Laterality of the Human Inferior Longitudinal Fasciculus. Front Neuroanat 12:47

40. Rokem A, Takemura H, Bock AS et al (2017) The visual white matter: the application of diffusion MRI and fiber tractography to vision science. J Vis 17:4
41. Rosa MG, Palmer SM, Gamberini M et al (2009) Connections of the dorsomedial visual area: pathways for early integration of dorsal and ventral streams in extrastriate cortex. J Neurosci 29:4548–4563
42. Seltzer B, Pandya DN (1984) Further observations on parieto-temporal connections in the rhesus monkey. Exp Brain Res 55:301–312
43. Smith SM, Beckmann CF, Andersson J et al (2013) Resting-state fMRI in the Human Connectome Project. NeuroImage 80:144–168
44. Stilla R, Sathian K (2008) Selective visuo-haptic processing of shape and texture. Hum Brain Mapp 29:1123–1138
45. Taylor JC, Downing PE (2011) Division of labor between lateral and ventral extrastriate representations of faces, bodies, and objects. J Cognit Neurosci 23:4122–4137
46. Thiebaut De Schotten M, Dell'acqua F, Forkel SJ et al (2011) A lateralized brain network for visuospatial attention. Nat Neurosci 14:1245–1246
47. Tootell RB, Reppas JB, Kwong KK et al (1995) Functional analysis of human MT and related visual cortical areas using magnetic resonance imaging. J Neurosci 15:3215–3230
48. Wall MB, Lingnau A, Ashida H et al (2008) Selective visual responses to expansion and rotation in the human MT complex revealed by functional magnetic resonance imaging adaptation. Eur J Neurosci 27:2747–2757
49. Wang Y, Fernandez-Miranda JC, Verstynen T et al (2013) Rethinking the role of the middle longitudinal fascicle in language and auditory pathways. Cereb Cortex 23:2347–2356
50. Wu Y, Sun D, Wang Y et al (2016) Subcomponents and Connectivity of the Inferior Fronto-Occipital Fasciculus Revealed by Diffusion Spectrum Imaging Fiber Tracking. Front Neuroanat 10:88
51. Wu Y, Sun D, Wang Y et al (2016) Tracing short connections of the temporo-parieto-occipital region in the human brain using diffusion spectrum imaging and fiber dissection. Brain Res 1646:152–159
52. Wysiadecki G, Clarke E, Polguj M et al (2018) Klingler's method of brain dissection: review of the technique including its usefulness in practical neuroanatomy teaching, neurosurgery and neuroimaging. Folia Morphol 78:455–466
53. Yeatman JD, Weiner KS, Pestilli F et al (2014) The vertical occipital fasciculus: a century of controversy resolved by in vivo measurements. Proc Natl Acad Sci USA 111:E5214–E5223
54. Yeh FC, Wedeen VJ, Tseng WY (2010) Generalized q-sampling imaging. IEEE Trans Med Imaging 29:1626–1635