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Anatomy and White Matter Connections of the Lingual Gyrus and Cuneus

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BACKGROUND: **The medial occipital lobe, composed of the lingual gyrus and cuneus, is necessary for both basic and higher level visual processing. It is also known to facilitate cross-modal, nonvisual functions, such as linguistic processing and verbal memory, after the loss of the visual senses. A detailed cortical model elucidating the white matter connectivity associated with this area could improve our understanding of the interacting brain networks that underlie complex human processes and postoperative outcomes related to vision and language.**

METHODS: **Generalized q-sampling imaging tractography, validated by gross anatomic dissection for qualitative visual agreement, was performed on 10 healthy adult controls obtained from the Human Connectome Project.**

RESULTS: **Major white matter connections were identified by tractography and validated by gross dissection, which connected the medial occipital lobe with itself and the adjacent cortices, especially the temporal lobe. The short- and long-range connections identified consisted mainly of U-shaped association fibers, intracuneal fibers, and inferior fronto-occipital fasciculus, inferior longitudinal fasciculus, middle longitudinal fasciculus, and lingual—fusiform connections.**

CONCLUSIONS: **The medial occipital lobe is an extremely interconnected system, supporting its ability to perform coordinated basic visual processing, but also serves as a center for many long-range association fibers, supporting its importance in nonvisual functions, such as language and memory. The presented data represent clinically actionable anatomic information that can be used in multimodal navigation of white matter lesions in the medial occipital lobe to prevent neurologic deficits and improve patients' quality of life after cerebral surgery.**

INTRODUCTION

The basic and complex visual processing in the primary visual area (V1) in the occipital lobe is sent to the extrastriate visual areas (V2-V4) and then to the adjacent cortices in dual, parallel streams.[1] The dorsal stream extends from V1 to the posterior parietal area and facilitates visuospatial coordination. The ventral stream extends from V1 to the temporal cortex to facilitate object recognition.[2] V1 surrounds the calcarine sulcus on the medial aspect of the occipital lobe, which is composed of the cuneus and lingual gyrus. More broadly, the cuneus and lingual gyri house functional areas of V1 to V4 and facilitate proper functioning of the ventral and dorsal streams.[3,4] These two gyri have been implicated in both the basic and the higher order visual processing required for the orientation and direction of stimuli,[5] color,[6] and faces.[7]

Preservation of the cortical tracts originating from the medial occipital lobe and extending to adjacent cortices is essential to maintain basic visual processing in patients after cerebral

Key words
- Anatomy
- DSI
- Occipital lobe
- Tractography
- White matter

Abbreviations and Acronyms
DSI: Diffusion spectrum imaging
FFA: Fusiform face area
IFG: Inferior frontal gyrus
IFOF: Inferior fronto-occipital fasciculus
ILF: Inferior longitudinal fasciculus
MdLF: Middle longitudinal fasciculus
ROI: Region of interest
V1: Primary visual area
V2-V4: Extrastriate visual areas

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surgery.[8,9] Numerous studies have also suggested a possible "supramodal" organization of the brain in which the primary cortices are dependent on functional specialization rather than on unimodal sensory information alone. In line with these observations, the lingual gyrus and cuneus have also demonstrated functional relevance in processes that included visual memory storage,[10] visual imagery,[11] creative thinking,[12] and linguistic processing.[10,13] Thus, clarification of the fiber bundle anatomy of the medial occipital lobe and its connections to the adjacent cortical regions could provide insight into the underlying complex processes supported by this region and also improve our ability to apply effective intraoperative brain mapping in the occipital lobe to reduce neurologic deficits and improve patients' quality of life.[14,15]

In the present study, we used diffusion spectrum imaging (DSI)-based tractography to study the structural organization and connectivity of the medial occipital lobe white matter tracts with our regions of interest (ROIs) as the lingual gyrus and cuneus. Tractography was performed using generalized q-sampling imaging (GQI) validated by gross anatomic dissection performed on 10 healthy, human brains, as previously reported.[16] An extensive literature review was also performed to elucidate the major functions facilitated by this cortex in the context of the network connectivity described in the present study. We have described our structural analysis of the medial occipital lobe according to the major connections and relations to other cortical structures to suggest how its connectivity might suggest function.

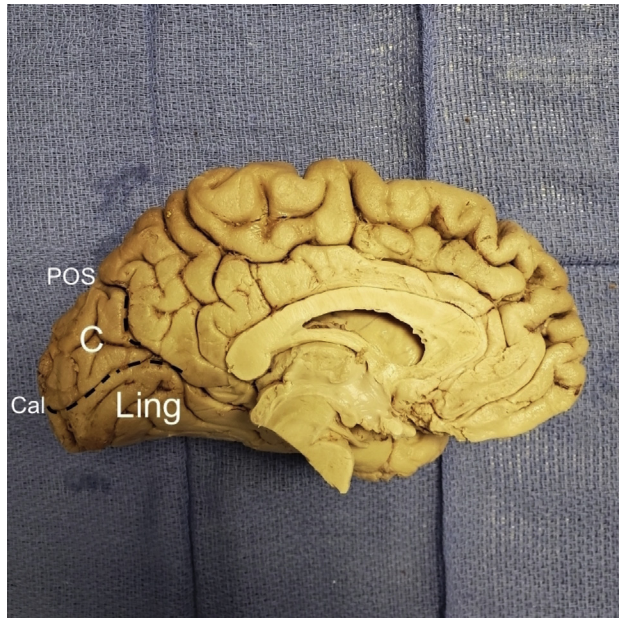

Figure 1. Borders of the lingual gyrus as seen with dissection. The cuneus (C) and the lingual gyrus (Ling) can be seen divided by the calcarine fissure (Cal) and their sulci. POS, posterior.

METHODS

Defining the ROIs

From an anatomical perspective, the lingual gyrus was named because of its resemblance of its shape to a tongue. It is located on the posteroinferior portion of the medial surface of the occipital lobe, reaching the occipital pole. It is bound by the calcarine fissure and posterior portion of the collateral sulcus. It courses anteriorly and merges with the parahippocampal gyrus at the tentorial surface of the temporal lobe (**Figure 1**).

The cuneus is also located on the medial surface of the occipital lobe. It shares a border with the lingual gyrus and is demarcated by the calcarine sulcus inferiorly. It extends posteriorly to form the dorsal surface of the occipital lobe. Anteriorly, it is bound by the parieto-occipital sulcus, which separates the cuneus from the precuneus. The triangular shape is shown in **Figure 1**.

Tractography

Neuroimaging data from 10 healthy adult controls were obtained from the Human Connectome Project (available at: http://humanconnectome.org; release Q3) for DSI-based tractography analysis in the present study. We used a multishell diffusion scheme with b-values equal to 990, 1985, and 1980 s/mm^2 and sampling in 90 directions for each b value.[17] The in-plane resolution and slice thickness were both 1.25 mm. A generalized GQI method was used for the diffusion data with a diffusion sampling length ratio of 1.25.[18]

The subjects were compared through registration of neuroimaging data to the Montreal Neurologic Institute (MNI) space on a simulated brain.[19] The tractography methods used in the present study have been elucidated in detail in previous studies.[16,17] Tractography was performed using the DSI Studio (University of Pittsburgh, Pittsburgh, Pa) with two predefined ROIs. ROIs were created in the superior, middle, and inferior occipital lobes. A second ROI was created in each individual gyri of the cerebral cortex, which allowed us to investigate all other white matter tracts between the medial occipital lobe and the rest of the cerebral cortex.

The ROIs were placed manually to isolate the major tracts. An ROI was created that demarcated the lingual gyrus, bound by the collateral sulcus and calcarine sulcus and anteriorly by the parahippocampal gyrus. The cuneus ROI created was demarcated by the calcarine sulcus and parieto-occipital sulcus and laterally by the interoccipital sulcus (which separates the cuneus from the superior occipital gyrus). All major fiber bundles reported in the present study were independently identified by a minimum of three of the current authors for all subjects studied. Tractography was completed before the cadaveric study.

Postmortem Dissection

Postmortem dissections were completed to demonstrate the location of the major tracts connecting the medial occipital lobe and for validation of our tractography results by qualitative visual agreement. The postmortem dissections were performed using a modified Klingler technique.[20] All tracts were dissected in both hemispheres for all regions of the lingual gyrus and cuneus. Ten specimens were used for the present study, which were obtained from the University of Oklahoma Health Science Center Willed Body Program with approval of the state's anatomical board. As previously elucidated,[16,17] specific care was taken to leave the cortical areas corresponding to the white matter tracts of interest intact to preserve their relationships. The tracts were dissected with blunt instruments to avoid disrupting the natural tract anatomy. Photographs were taken at each stage of the dissection.

RESULTS

Intraoccipital Connections

U-Shaped Fibers. U-shaped fibers are ubiquitous between adjacent gyri. Starting from the posterior portion of the lateral aspect of the gyrus, at the collateral sulcus, the expected connections were found between the lingual gyrus and the adjacent fusiform gyrus. These fibers take an inverted U-shape. They start at the inferior aspect of the posterolateral portion of the lingual gyrus, loop upward around the collateral sulcus, and end in the medial portion of the fusiform gyrus.

These U-shaped fibers are also present between the lingual gyrus and cuneus. The fibers, centered around the calcarine sulcus, course from the inferior portion of the cuneus and take a U-shaped bend around the calcarine sulcus to end in the superior portion of the lingual gyrus (Figure 2). They are unique in that they are present in a successive series around the calcarine sulcus until they reach the end of the calcarine sulcus (adjacent to the posterior cingulate area). U-shaped fibers were also present between the cuneus and the superior occipital gyrus. These fibers are separated by the interoccipital sulcus.

Lingual-Fusiform Connections. Fibers that connected the lingual gyrus to the fusiform gyrus were also detected. These fibers originated at the posteromedial portion of the lingual gyrus,

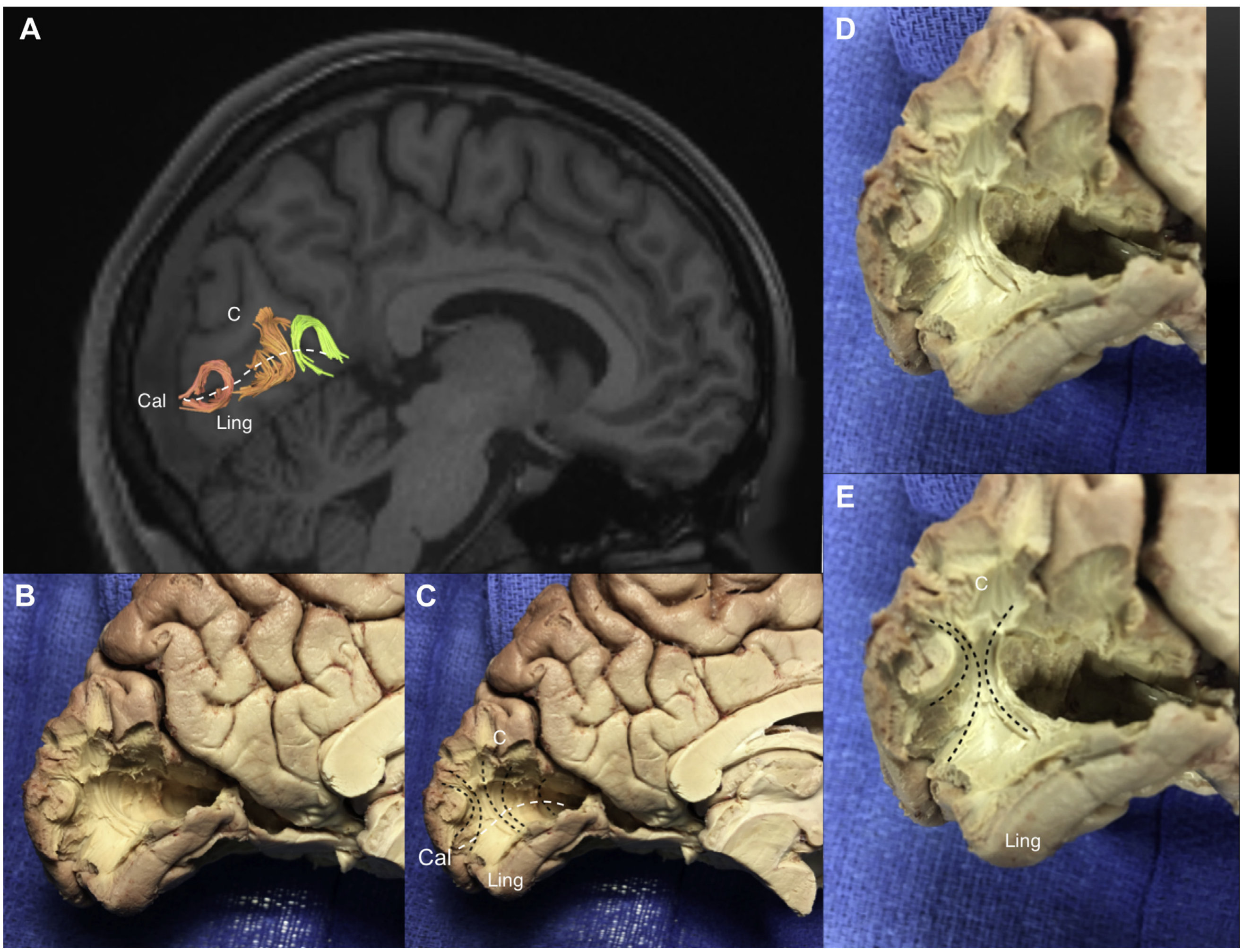

Figure 2. An example of U-shaped fibers in the medial occipital lobe. (**A**) Between the lingual gyrus (Ling) and the cuneus (C), the U-shaped fibers are present in a series in an anteroposterior fashion along the calcarine sulcus (Cal) on tractography (seen in *red, orange,* and *green*). The U-fibers seen by tractography (**A**) were visually confirmed by gross dissection. (**B**–**E**).

coursed anteriorly over the collateral sulcus, and ended in the anterior portion of the fusiform gyrus, adjacent to the collateral sulcus (Figure 3).

Intracuneal Fibers. The cuneus was found to have extensive connections within the gyrus. The fibers that coursed in a superoinferior plane along the gyrus were observed with tractography and confirmed by dissection. These fibers had one end in the calcarine sulcus, coursing superiorly to the parieto-occipital sulcus. These were present over most of the cuneus, but were focused at the posterior half of the cuneus (Figure 4).

Long Range Association Fibers

Inferior Longitudinal Fasciculus. The association fibers of the lingual gyrus and cuneus include the inferior longitudinal fasciculus (ILF) and the inferior fronto-occipital fasciculus (IFOF). The fibers of the ILF have one origin in the entire posteromedial aspect of the lingual gyrus and cuneus. The fibers then course anteriorly, staying lateral to the occipital horn of the lateral ventricle. Once in the temporal lobe, these fibers remain lateral to the temporal horn of the lateral ventricle, terminating in the temporal pole (Figure 5). We have demonstrated that the fibers of the ILF from the lingual gyrus terminate more inferiorly in the temporal pole and inferior temporal gyrus compared with the ILF fibers from the cuneus, which primarily end in the superior temporal gyrus.

Inferior Fronto-Occipital Fasciculus. The IFOF has fibers that also have an origin over the entire aspect of the posteromedial aspect of the lingual gyrus and the cuneus. It initially runs with the commissural fibers (see the section "Projections Through the Corpus Callosum") and the ILF, traveling anteriorly. From the lingual gyrus, these fibers travel along the inferolateral aspect of the occipital horn of the lateral ventricle. These fibers then stay lateral to the temporal horn of the lateral ventricle in the temporal lobe and course back medially and pass superiorly over the temporal horn of the ventricle to reach the insula. The IFOF then passes through the short gyri of the insula and courses into the frontal lobe, primarily into the inferior frontal gyrus (IFG; ie, pars orbitalis and pars operculum primarily) and the orbitofrontal cortex.

The cuneus is the major contributor to the IFOF. The occipital end of the IFOF has its main starting points all along the dorsomedial surface of the occipital lobe that span from the calcarine sulcus to the parieto-occipital sulcus. These fibers stay superior to the lingual gyrus IFOF fibers as the border the ventricle. Additionally, they were found to differ in that most of their fibers

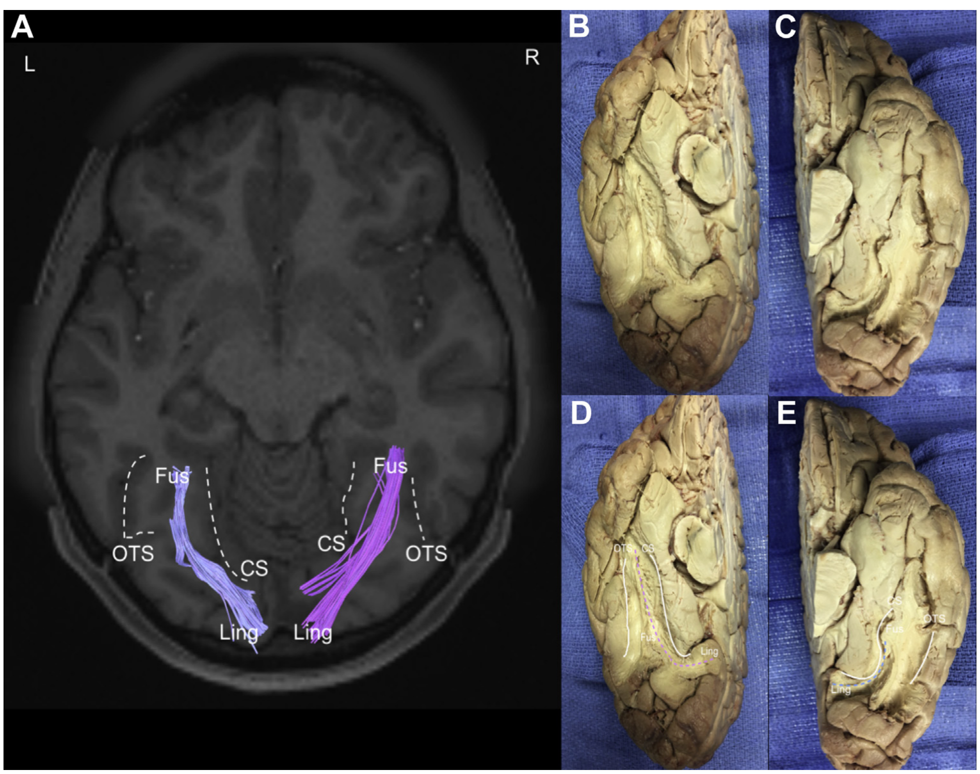

Figure 3. White matter pathways between the lingual fusiform gyri. (**A**) On tractography, we found that the lingual gyrus (Ling) has connections that originate from the calcarine sulcus (CS) and course to the medial aspect of the fusiform gyrus (Fus). (**B**–**E**) During gross dissection, the gray matter and the collateral sulcus were removed to reveal the white matter between the lingual gyrus and fusiform gyrus. OTS, occipitotemporal sulcus.

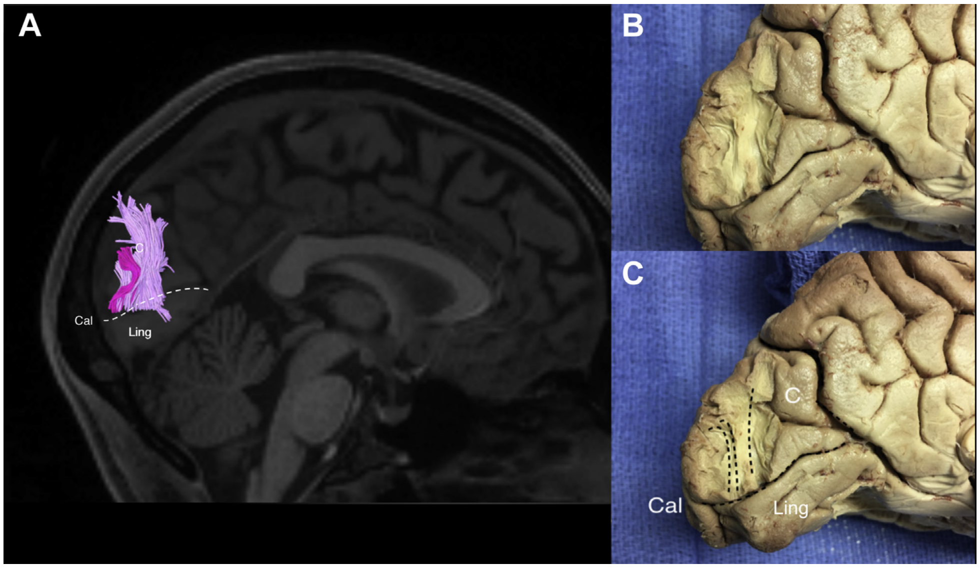

Figure 4. Fibers within the cuneus. (**A**) Intracuneal fibers are seen by tractography connecting extensively in a superoinferior plane along the gyrus. These fibers can be seen coursing superiorly towards the parieto-occipital sulcus. (**B** and **C**) These connections were also confirmed by gross dissection. C, cuneus; Cal, calcarine sulcus; Ling, lingual gyrus.

terminated in the superior frontal gyrus. The IFOF is shown in Figure 6.

Connections with the Parahippocampal Gyrus. Connections were also noted between the cuneus and the parahippocampal gyrus. These fibers remain on the medial portion of the occipital horn of the ventricle and then continue into the parahippocampal gyrus, ending at the anterior portion of the parahippocampal gyrus (Figure 7).

Projections Through the Corpus Callosum. Commissural fibers are found in the lingual gyrus. These fibers have an origin in the posteromedial aspect of the lingual gyrus and the cuneus. They course anteriorly, staying on the medial aspect of the occipital horn of the lateral ventricle. Near the trigone, they bend in the coronal plane, medially 90°, and pass through the splenium of the corpus callosum. The fibers then bend 90° again, in a symmetric fashion, staying medially to the contralateral occipital horn and head back toward the posteromedial occipital lobe in a symmetric fashion. The fibers primarily end at the contralateral posteromedial aspect of the lingual gyrus and the cuneus. The commissural fibers, and their relation to the optic radiations, discussed in the next section, are demonstrated in Figures 8 and 9.

Optic Radiations. The optic radiations have been shown to start from the lateral geniculate nucleus. The optic radiations then course laterally to reach the lateral aspect on the atrium. From there, they course straight back to the lingual gyrus and cuneus. The fibers of the optic radiations synapse along the dorsomedial aspect of the cuneus, from the parieto-occipital sulcus to the calcarine sulcus. The optic radiations also have fibers that span the dorsomedial aspect of the lingual gyrus, starting at the calcarine sulcus and reaching the inferior limit of the gyrus (Figure 10).

Middle Longitudinal Fasciculus. Tractography demonstrated that a portion of the middle longitudinal fasciculus (MdLF) had one end in the medial occipital lobe as it coursed to the superior temporal gyrus. One end of the MdLF was demonstrated to have an origin in the superior occipital lobe, along with the lingual gyrus and cuneus. These fibers then course downward, running in the inferior parietal lobe, and staying lateral to the atrium of the lateral ventricle. From the temporoparietooccipital junction, and then Heschl's gyrus, most of these fibers course directly into the anterior portion of the superior temporal gyrus, stopping short of the temporal pole (Figure 11).

DISCUSSION

In the present study, we have demonstrated the underlying cortical anatomy of the medial occipital lobe, a region of the cerebral cortex that holds the cuneus and lingual gyrus and facilitates visual processing.[5] Although functional information is beneficial to understanding the neural basis of complex behaviors such as selective object recognition,[21] additional information is necessary to understand the cortical anatomy of the medial occipital lobe and its clinical relevance to cerebral surgery.

The medial occipital lobe is an extremely interconnected system, which might explain its ability to perform coordinated basic visual processing. However, the medial occipital lobe is also the center of many long-range association fibers, which supports roles that extend past basic visual processing.[10] In glioma surgery, it is essential to preserve the key connections between the components

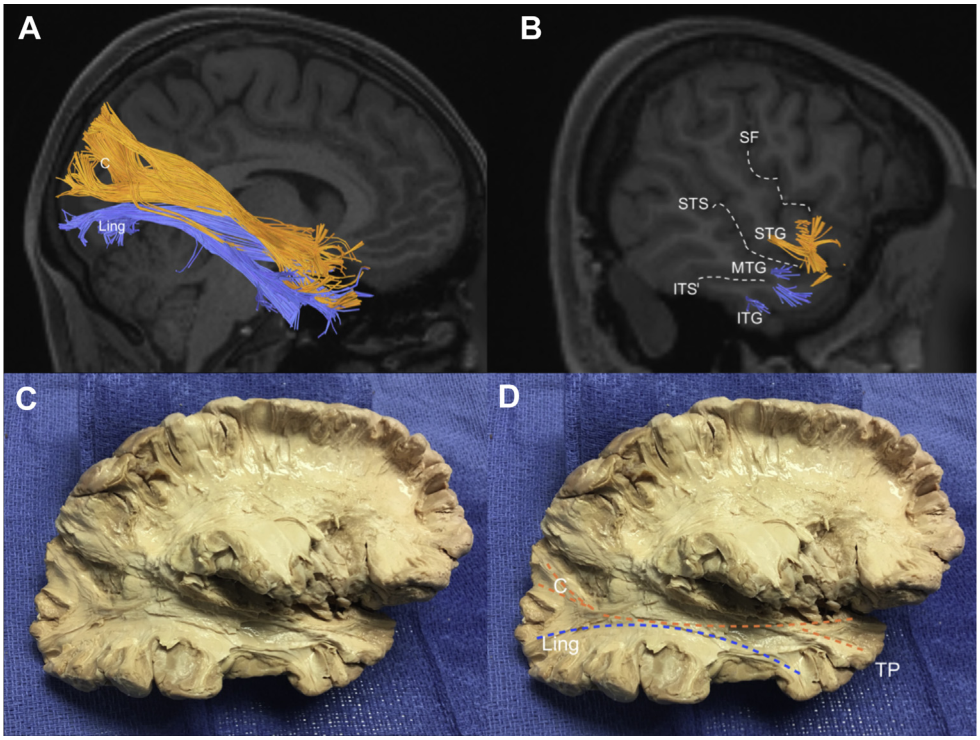

Figure 5. The inferior longitudinal fasciculus (ILF) from the cuneus (C) and lingual gyrus (Ling). The ILF fibers from the lingual gyrus (*blue*) terminated in the temporal pole toward the inferior temporal gyrus (ITG), remaining more inferior to those of the cuneus (*orange*), which extended more toward the superior temporal gyrus (STG). Findings on tractography (**A** and **B**) are confirmed with gross dissection (**C** and **D**). MTG, middle temporal gyrus; SF, sylvian fissure; STS, superior temporal sulcus; TP, temporal pole.

of the functional networks, but still maximize the extent of resection to optimize the oncological—functional balance in patients.[15,22] Therefore, in the present study, we used GQI-based tractography, validated by gross anatomic dissection, to elucidate the connections of the medial occipital lobe in 10 normal subjects and discussed its functional relevance in the context of the reported data.

Functional Studies

Visual Processing. The cuneus and lingual gyrus house the functional areas V1-V4, which are associated with basic visual processing. V1, located on the banks of the calcarine sulcus, is associated with processing the visual stimuli detected in the visual field, mainly the fovea, in an inverted contralateral fashion.[4,23] Area V2 divides the visual field into two discontinuous contralateral inverted quarter fields, and areas V3 and V4 are required to incorporate more of the peripheral visual fields.[4,23]

Multiple functional studies have demonstrated that the cuneus is involved in basic visual processing tasks such as spatial frequency, orientation, motion, direction, and speed.[5,21,24] Other functional studies have demonstrated that the lingual gyrus is preferentially activated when displaying words under lower contrast and is involved in direction and motion discrimination.[3,12] The hierarchal organization of the visual cortex might demonstrate a reversed organization in individuals who lose their visual sensory functions at an early age (ie, "early blindness"), suggesting a high capability for plasticity in these regions to facilitate nonvisual processing after cortical damage, such as in verbal memory and linguistic processing (see the section "Linguistic Processing and Plasticity").[10]

Facial Processing. The processing of high-order visual information, such as faces, likely requires input from multiple, interacting neural networks, rather than just individual cortical regions, such as the fusiform face area (FFA).[25] In line with this hypothesis, the lingual gyrus and cuneus are involved in face recognition and the complex processing of emotional expression.[7] Given the proximity of the lingual gyrus to the FFA in the fusiform gyrus, it has been expected that adjacent areas in the occipital lobe are simultaneously involved in facial processing.[17,23] A principle component analysis using functional magnetic resonance imaging data from 14 healthy human subjects demonstrated distinct, but interacting, roles for the fusiform gyrus and lingual gyrus for the complex function of facial processing. Thus, the fusiform gyrus might facilitate detection of emotional facial expressions while the lingual gyrus might be more necessary for initial facial identification.[7] Improved understanding of the structural and functional connectivity of the lingual gyrus and

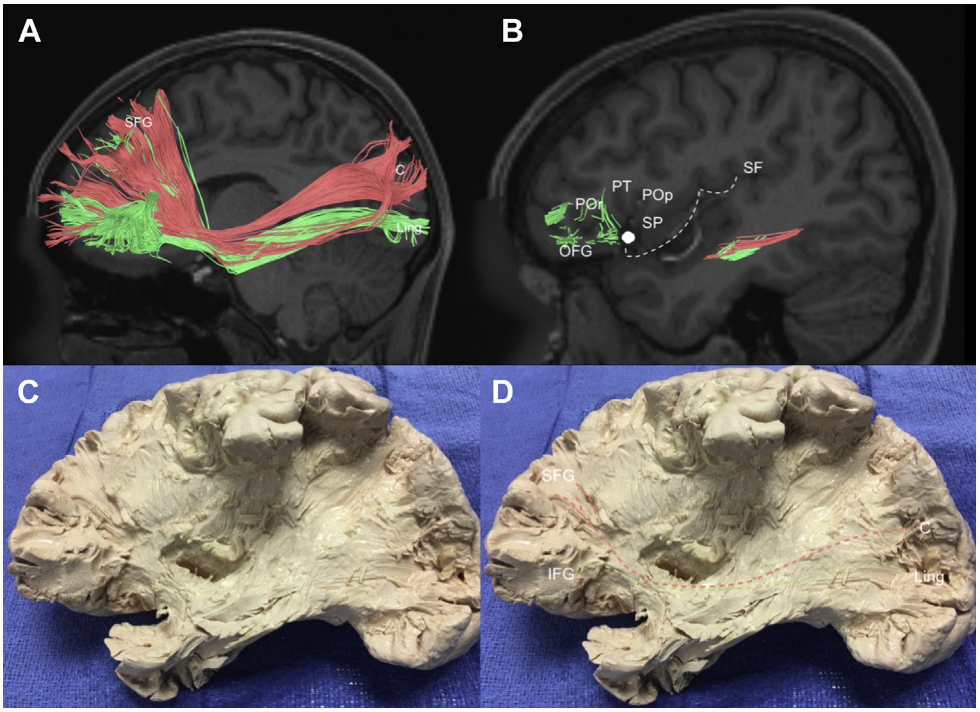

Figure 6. The inferior fronto-occipital fasciculus (IFOF) from the lingual gyrus (Ling) and cuneus (C). Fibers from the cuneus (*red*) can be seen terminating in the superior frontal gyrus (SFG), with the fibers from the lingual gyrus (*green*) terminating in the inferior frontal gyrus (IFG). Findings on tractography (**A** and **B**) are confirmed with gross dissection (**C** and **D**). OFG, orbitofrontal gyrus; PO, pars orbitalis; POp, pars opercularis; PT, pars triangularis; SF, sylvian fissure; SP, sylvian point.

cuneus in a "facial network" could help explain neurologic deficits resulting in impaired facial processing, such as in prosopagnosia.

Visual Memory and Emotion. The lingual gyrus has also been implicated in visual memory and emotion.[12] It is understood that damage to the occipital lobe can lead to selective visual amnesia.[26] Similarly, patients with bilateral ischemic strokes of the lingual gyrus have demonstrated impairments in visual learning, implicating its involvement in visual memory.[9] Relative gray matter volume studies have also demonstrated that the lingual gyrus is associated with visual memory storage.[12] Thus, measuring the lingual gyrus gray matter volume has provided an opportunity to detect the early markers of neurocognitive performance and long-term memory decline.[12,27]

Given the complex relationship of emotion in learning and memory, it is unsurprising that these cortical areas might have additional roles in emotional regulation. The lingual gyrus and cuneus are necessary for higher order visual processing, including the processing of emotional facial expressions.[7] Similarly, patients with major depressive disorder have displayed differences in global and local cortical separation distances in the right lingual gyrus compared with healthy controls.[28] Additional studies have implicated the activation of the lingual gyrus with the perception of pain, suggesting a possible role of this cortical region in the control of specifically *negative* emotions associated with painful events.[29,30] Thus, the lingual gyrus might facilitate both the control of emotion and the encoding of visual imagery according to the stimuli presented to it.

Creative Thinking, Visual Imagery, and Semantic Relatedness. Relative gray matter volume studies have also investigated markers of creative potential. They have demonstrated that divergent thinking (creative thinking) is related to the gray matter volume in the IFG, superior frontal gyrus, inferior parietal lobule, precuneus, and cuneus.[27,31] The cuneus and lingual gyrus have been linked to visual imagery, which is necessary in the creative thinking process.[11,12,27] Similarly, the ability to generate a creative thought has been linked to idea generation (ie, generating uncommon concepts from semantic memory) and proper idea evaluation (ie, screening ideas through inhibitory functions).[12] Too much inhibition can lead to the lack of creative potential. Therefore, a flexible adaption of inhibitory control is believed to be crucial for generating creative thoughts.

Is visual imagery the only method by which we generate creative potential? The left IFG and left lingual gyrus have essential roles in establishing the novelty-based representations required for the inventive process.[32] The left IFG is required for the generation of new semantic representation in the creative process, and the left lingual gyrus and cuneus are necessary for presenting new visual imagery in the processing of semantic relatedness (how related

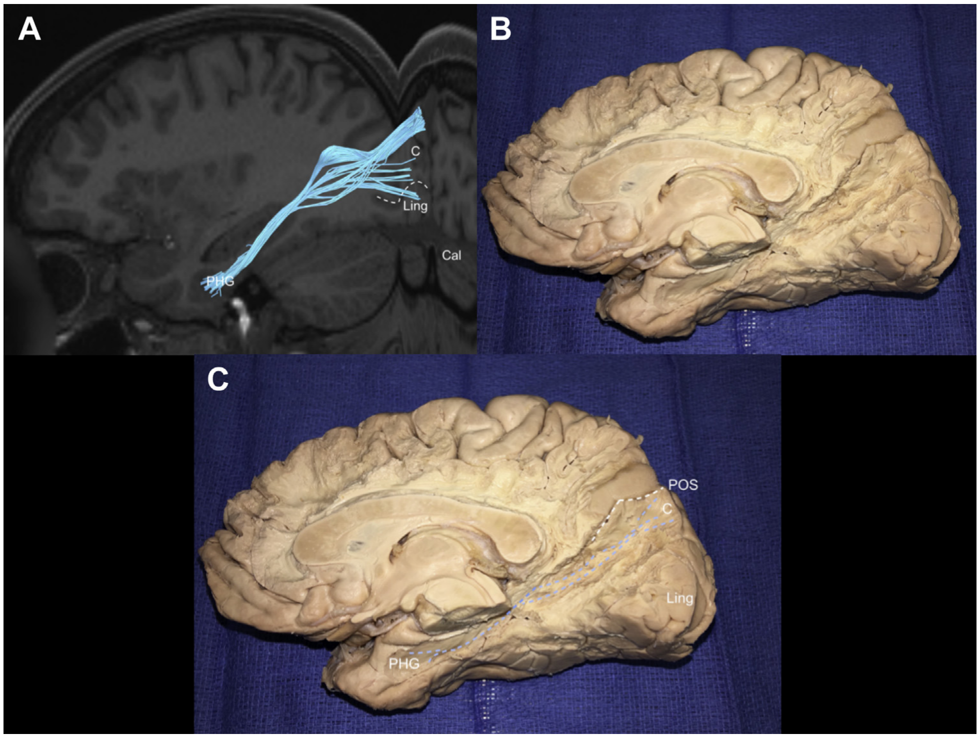

Figure 7. Connections between the medial occipital lobe and parahippocampal gyrus (PHG). These fibers (*blue*) can be seen originating from the posterior (POS) cuneus (C) and lingual gyri (Ling) before coursing along the medial portion of the occipital horn and terminating at the anterior portion of the parahippocampal gyrus. Findings on tractography (**A**) are confirmed with gross dissection (**B** and **C**).

sets of words or concepts are) for the creative process.[32] This observation supports the role of the lingual gyrus and cuneus in verbal memory because the processing of familiar semantic relatedness requires the retrieval of semantic information stored in long-term memory.

Linguistic Processing and Plasticity. The occipital cortex is often considered a unimodal region for visual processing. However, the primary visual cortex can demonstrate cross-modal, plastic changes in individuals with early visual losses occurring during a critical period when key connections are known to be established to support functional-specific roles rather than sensory-specific roles, such as linguistic processing.[10,13] A coordinate-based meta-analysis of 166 individuals with early blindness (the loss of vision before 6 years of age) found consistent activation of the cuneus and lingual gyrus for language processing tasks, such as braille reading, verbal memory, and sentence completion.[10] Specifically, the left lingual gyrus and left cuneus were the most activated regions in those with early blindness for language-related tasks, similarly reflecting the left lateralization of the language network. The right lingual gyrus and cuneus were more activated for spatially related tasks compared with healthy controls.[10]

Given the language network is especially plastic when key connections are being formed early in life,[33] the cuneus and lingual gyrus might be incorporated into the language network after early visual losses.[10] These results are supported by the observation that repetitive transcranial magnetic stimulation of the occipital pole disrupts verb generation in blind individuals but not in healthy, normally sighted, individuals.[13] Similarly, occipital lesions can abolish the ability to read braille.[34] The visual cortex might have a topographical organization in blind individuals, with the posterior regions, including the cuneus, more responsible for verbal memory and tactile-based tasks such as braille reading facilitated by anterior regions of the occipital cortex.[35] Nonetheless, these observations support the highly valuable research required for intraoperative brain mapping to safely maximize the extent of resection and also subsequent neurorehabilitation after surgery to allow for functional compensation in patients with tumors in these cortical areas.[14] The findings presented in the current study have provided insight into those processes.

Relation of Tractography Findings to Gross Dissection and Functional Study Findings

U-Shaped Fibers and Intracuneal Fibers. Our tractography and dissection studies revealed many local connections within the cuneus. These were expected results owing to the requirement to process visual stimuli, because we expected that extensive connections would be present within the occipital lobe. This supports

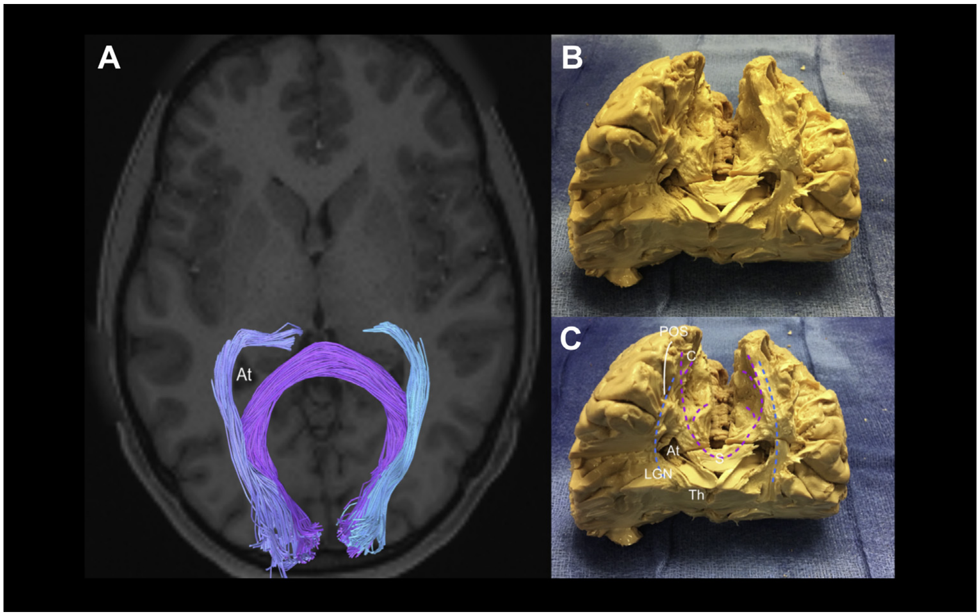

Figure 8. The callosal fibers (*purple*) in relation to the adjacent optic radiations (*blue*). The callosal fibers will stay medial to the ventricle and then cross the splenium before ending in an adjacent portion of the occipital lobe. The optic radiations remain lateral to the atrium (At) of the lateral ventricle. Findings on tractography (**A**) are confirmed with gross dissection (**B** and **C**). LGN, lateral geniculate nucleus; Th, thalamus.

the multiple previously cited functional studies that have demonstrated that the cuneus is involved in basic visual processing functions such as spatial frequency, orientation, motion, direction, and speed.[5,21,24]

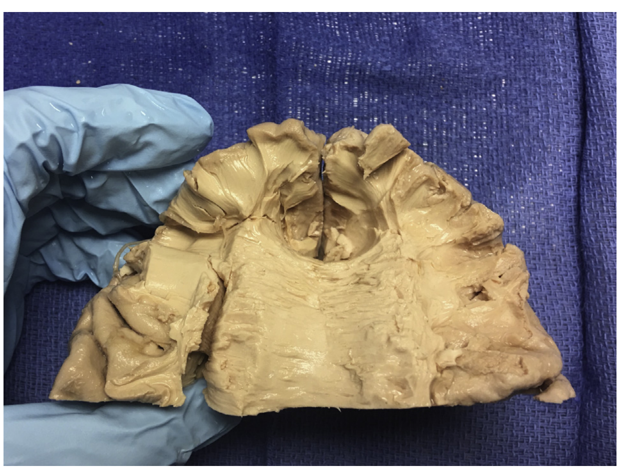

Figure 9. Gross anatomic representation of the optic radiations and commissural fibers. Optic radiations can be seen coursing from the lateral geniculate nucleus of the thalamus to the posterior portion of the medial occipital lobe.

The series of U-shaped fibers along the calcarine sulcus also supports the extensive amount of visual processing that begins within the V1. These fibers, along with the forceps/callosal fibers, demonstrate how the medial occipital lobe is able to perform numerous basic visual processing functions. How these numerous fibers come together to support visual processing is unknown and can only be conjectured from functional studies.

Lingual—Fusiform Fibers. Our tractography and dissection studies also revealed connections between the lingual gyrus along the calcarine sulcus and the fusiform gyrus. These connections were detected between V1 and the medial aspect of the fusiform gyrus adjacent to the FFA. The FFA receives static and dynamic details of invariant components of facial features.[4,23] The lingual gyrus has also been implicated in the processing of facial features. The findings from these functional studies, combined with our results, suggest that the lingual gyrus begins the task of processing facial information and feeds into the FFA for more detailed processing to achieve a holistic sense of the face.

Medial Occipital Lobe and Medial Temporal Lobe. From the major white matter tract of the medial occipital lobe, the ILF, we found that some fibers diverged and coursed toward the parahippocampal gyrus, adjacent to the amygdala and the hippocampus. This was also an expected result, because studies have linked the lingual gyrus and cuneus with visual memory.

Inferofrontal Occipital Fasciculus. The IFOF was one of the major white matter tracts we were able to dissect in the medial occipital

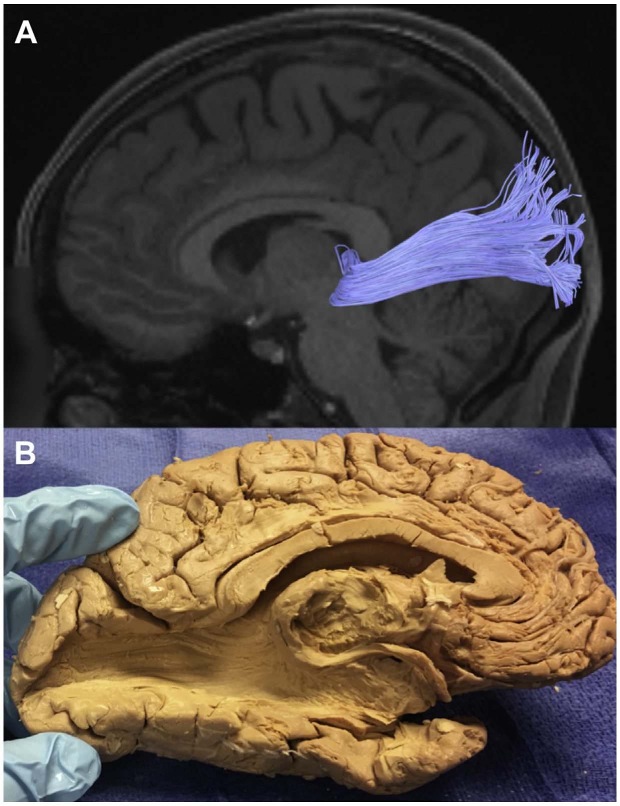

Figure 10. Illustration of the optic radiations in relation to the commissural fibers. (**A**) By tractography, the optic radiations (*blue*) can be seen coursing from the lateral geniculate nucleus of the thalamus to the posterior portion of the medial occipital lobe. (**B**) These results were confirmed by gross dissection.

lobe. Our tractography and dissection findings demonstrated that most of the IFOF that originated from the cuneus had frontal connections to the superior frontal gyrus. In contrast, most of the IFOF the originated from the lingual gyrus had frontal connections in the inferior frontal gyrus and orbitofrontal gyrus.

Many functions have been associated with the IFOF. Functional studies have demonstrated that the IFOF and lingual gyrus are important for semantic relatedness.[32,36] Moritz-Gasser et al[37] expanded on this by demonstrating, through nonverbal semantic association tasks, that the IFOF is important for multimodal semantic processing. Knowing that the lingual gyrus has been associated with semantic processing and observing that the IFOF has a lingual gyrus subdivision that primarily has connections within the inferior frontal gyrus and orbitofrontal gyrus, it can be postulated that this portion of the IFOF might establish semantic relatedness, especially for orthographic stimuli.

Does the IFOF contribute to creative thinking? Previously cited studies have shown that the cuneus is important for generating visual imagery. The IFOF's role in executive functioning, supported by studies of addiction and obsessive-compulsive disorder, and its connections to the frontal lobe have demonstrated its ability to receive stimuli and filter them.[29,38] The IFOF might be able to receive ideas generated through visual imagery in the cuneus and inhibit them in such a pattern to generate creative thought. This might be the predominant role of the cuneal portion of the IFOF. The IFOF has also been implicated in reading functions (discussed in the next section).

Inferior Longitudinal Fasciculus. Our tractography and dissection findings have demonstrated that the ILF connects the medial occipital lobe and anterior temporal pole. The ILF has been tested with intraoperative stimulation, and it has been demonstrated to elicit transient visual agnosia.[39] This was an expected finding owing to the tract's proximity to the visual ventral stream and suggests that the ILF has a role in visual processing and the identification of stimuli.

Therefore, does it follow that the ILF is important for semantic processes? One study demonstrated that the properties of the ILF and uncinate fasciculus were predicative of successful word learning.[39] Hodgetts et al[40] has supported these findings by demonstrating that the ILF correlated with the quality of semantic autobiographical memory. This could be expected from the anatomical position of the ILF, because it connects the occipital lobe (word—object recognizer) with the temporal lobe (important for memory).

The ILF has also been implicated in the function of reading. Mandonnet et al[41] demonstrated that damage to the ILF will result in impaired naming and fluency, although temporarily. The ILF, as reported by previously cited studies, is important for creating a semantic database from which lexical retrieval can occur and visual identification. Therefore, it seems to be a strong candidate to support the reading network.[39,40] What is not known however, is why this reading dysfunction is only temporary.[41]

Middle Longitudinal Fasciculus. Our dissection findings demonstrated that the MdLF is present in the medial occipital lobe. This dissection was performed in all the brains and reliably demonstrated that the MdLF extended from the superior temporal gyrus to the lateral occipital lobe (mainly the superior occipital gyrus), medial occipital lobe (cuneus), and precuneus.

Some studies have proposed that the MdLF might support the integration of audio and visual input for the purpose of object recognition.[42] This might explain why the IFOF, although located primarily in the occipital lobe, is important for multimodal semantic processing. The MdLF, in the medial occipital lobe, interdigitates with the IFOF and the ILF. Its close association, along with the numerous local connections, might allow for audiovisual integration into pathways for semantic relatedness and memory.

CONCLUSIONS

The medial occipital lobe has functional areas that have been linked to receiving inputs from the visual field and performing

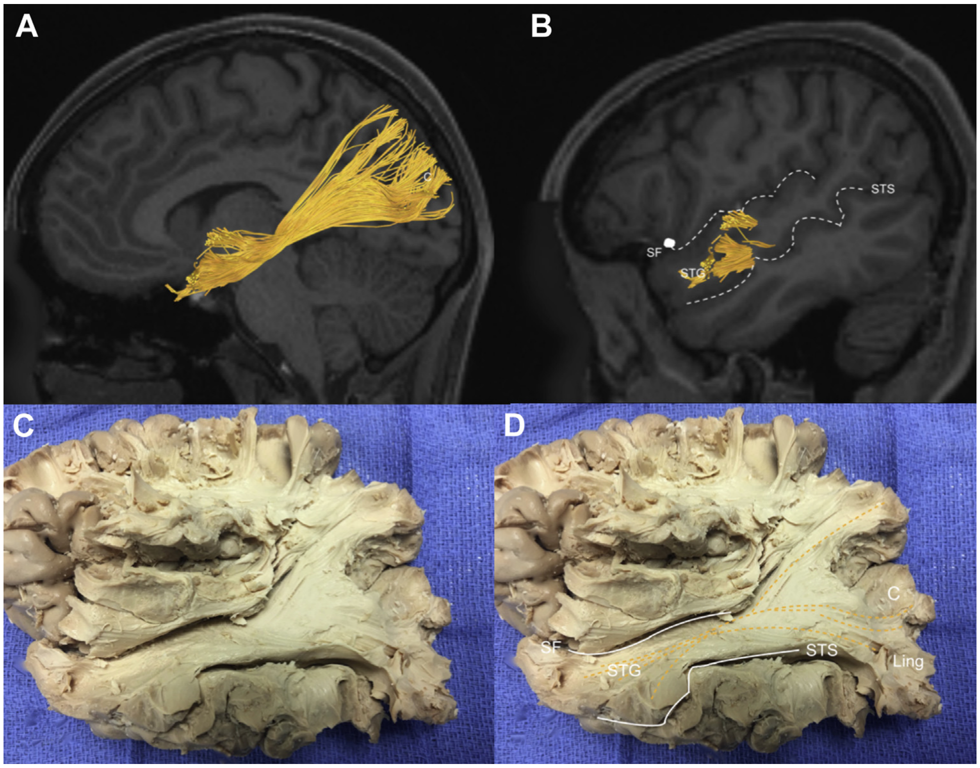

Figure 11. Middle longitudinal fasciculus (MdLF) in the medial occipital lobe. The MdLF (*pink*) has some extensions past the parieto-occipital sulcus (into the precuneus) and courses into the anterior superior temporal gyrus, falling short of the temporal pole. Findings on tractography (**A** and **B**) are confirmed with gross dissection (**C** and **D**). SF, sylvian fissure.

basic visual processing functions. Using DSI-based tractography, with the findings validated by those from gross dissection, we demonstrated the extent of the local interconnectedness of this portion of the occipital lobe. We demonstrated that many long range association fibers are present that might interact with visual processing to subserve semantic memory and relatedness.

CRediT AUTHORSHIP CONTRIBUTION STATEMENT

Ali H. Palejwala: Writing - original draft, Investigation. **Nicholas B. Dadario:** Writing - original draft, Formal analysis. **Isabella M. Young:** Writing - review & editing, Visualization. **Kyle O'Connor:** Investigation. **Robert G. Briggs:** Methodology. **Andrew K. Conner:** Writing - review & editing. **Daniel L. O'Donoghue:** Investigation, Visualization. **Michael E. Sughrue:** Conceptualization, Supervision.

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