A Connectomic Atlas of the Human Cerebrum—Chapter 6: The Temporal Lobe

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In this supplement, we build on work previously published under the Human Connectome Project. Specifically, we show a comprehensive anatomic atlas of the human cerebrum demonstrating all 180 distinct regions comprising the cerebral cortex. The location, functional connectivity, and structural connectivity of these regions are outlined, and where possible a discussion is included of the functional significance of these areas. In part 6, we specifically address regions relevant to the temporal lobe.

KEY WORDS: Anatomy, Cerebrum, Connectivity, DTI, Functional connectivity, Human, Parcellations

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The temporal lobe regions have traditionally been described and referred to in our field based on gross anatomy, namely gyral-based anatomy, with terms like T1 and T2 used as landmarks for comparative cross study communication. Connectomics informs us that such a system oversimplifies the real nature of the temporal lobe, which has numerous distinct cortical regions, many of which do not conform to sulcal boundaries, and many of which subdivide gyri into several subregions.

Despite these differences, temporal subdivisions mostly parallel the general anterior-to-posterior direction of the 5 temporal gyri: the superior temporal gyrus (STG), the middle temporal gyrus (MTG), the inferior temporal gyrus (ITG), the fusiform gyrus, and the parahippocampal/entorhinal gyri. Thus, they are explained in this manner in this text to facilitate organization and learning.

ABBREVIATIONS: EC, entorhinal cortex; **ILF,** middle longitudinal fasciculus; **ITG,** inferior temporal gyrus; **MdLF,** middle longitudinal fasciculus; **MR,** magnetic resonance; **MTG,** middle temporal gyrus; **PeEC,** perirhinal ectorhinal cortex; **PHA1,** parahippocampal area 1; **PHA2,** parahippocampal area 2; **PHA3,** parahippocampal area 3; **ProS,** prostriate region; **RSC,** retrosplenial cortex; **SLF,** superior longitudinal fasciculus; **STG,** superior temporal gyrus; **STS,** superior temporal sulcus; **STSda,** superior temporal sulcus dorsal anterior; **STSdp,** superior temporal sulcus dorsal posterior; **STSva,** superior temporal sulcus ventral anterior; **STSvp,** superior temporal sulcus ventral posterior; **TE,** temporal area; **TE1a,** temporal area 1 anterior; **TE1m,** temporal area 1 middle; **TE1p,** temporal area 1 posterior; **TE2a,** temporal area 2 anterior; **TE2p,** temporal area 2 posterior; **VVC,** ventral visual complex

BASIC ORGANIZATIONAL SCHEME OF THE TEMPORAL AREAS

In this new scheme, they are predominantly a reorganization of areas temporal area (TE), TF, and TG.[1] TE areas are further subdivided into TE1 and TE2. TE1 areas basically lie on the MTG, and TE2 areas lie on the ITG. It is important to note that they often cross sulci and gyral boundaries. TG areas are comprised of the temporal polar region. TF is primarily centered in the fusiform gyrus.

The STG areas are named differently, and many were discussed in the section on the insular and opercular regions (Chapter 5). The superior and superolateral surfaces of the STG are made up of auditory association cortices, like A4 and A5, and anterior regions such as TA2 and STGa. There are 4 specific regions (superior temporal sulcus dorsal anterior (STSda), superior temporal sulcus dorsal posterior (STSdp), superior temporal sulcus ventral anterior (STSva), and superior temporal sulcus ventral posterior (STSvp)) that are centered around the superior temporal sulcus (STS) and that overlap onto the visible surface of the inferior STG.

Similarly, and not surprisingly, the areas involved with the medial temporal cortices (parahippocampal and entorhinal cortices) are

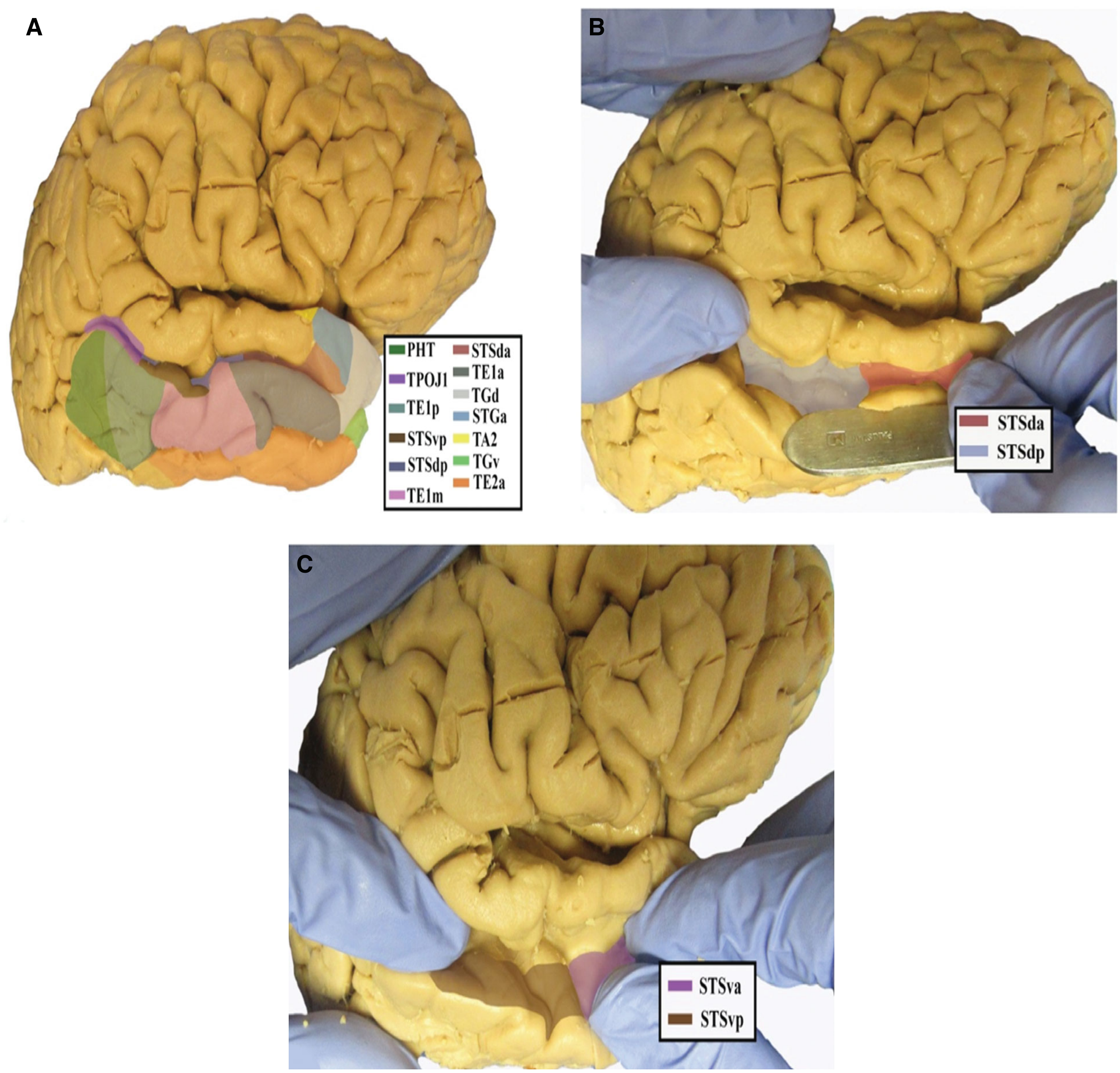

FIGURE 1. *Anatomic view of the STS parcellations shown on the right hemisphere of a cadaver brain.* **A**, *Lateral view of the temporal lobe.* **B**, *Lateral view of the temporal lobe with widening of the superior bank of the STS to show the extent of STSda and STSdp.* **C**, *Lateral view of the temporal lobe with widening of the inferior bank of the STS to show the extent of STSva and STSvp.*

distinct, and named outside the TE, TF, and TG system. While there are no specific reasons to suggest that TE1 areas are more linked to each other than TE2 areas, we have organized our discussion around this scheme to simplify its presentation.

STS Areas

The anatomic locations of the pacellations that comprise the STS are shown in Figure 1. The parcellations include STSda, STSdp, STSva, and STSvp. The combined tractography of the parcellations is shown in Figure 2.

Area STSda

Where is it? Area STSda is found on the anterior half of the lateral face of the STG and the anterior half of the superior bank of the STS.

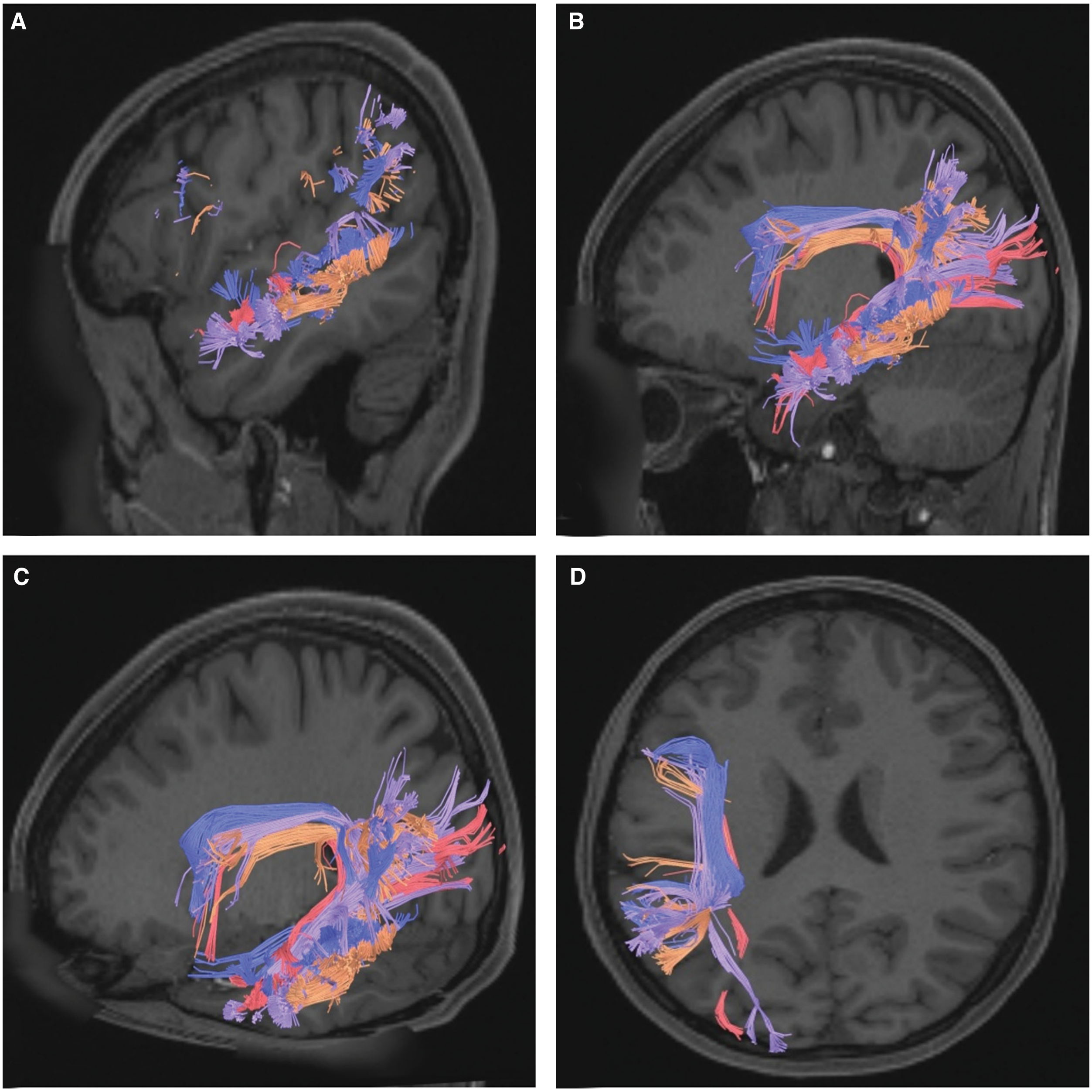

FIGURE 2. *Combined structural connectivity of the STS parcellations, shown on T1-weighted magnetic resonance (MR) images.* **A** *to* **C**, *Three sagittal views from* **A**, *most lateral to* **B**, *and* **C**, *most medial.* **D**, *Axial view. Tracks correspond to STSda (red), STSdp (blue), STSva (purple), and STSvp (orange).*

What are its borders? Area STSda borders area STSdp posteriorly, STSva and TGd inferiorly and anteroinferiorly, STGa anteriorly, and TA2 and A5 superiorly.

What is its functional connectivity? Area STSda demonstrates functional connectivity to areas 9m, 45, 47L, SFL, and 55b in the frontal lobe, areas STV, PSL, A5, and STGa in the insula opercular area, areas STSva, STSvp, STSdp, TGd, and TE1a in the temporal lobe, and areas PGi and 31pd in the parietal lobe (Figure 3).

What are its white matter connections? Area STSda is structurally connected to the arcuate/superior longitudinal fasciculus (SLF), middle longitudinal fasciculus (MdLF), and the "u" fibers

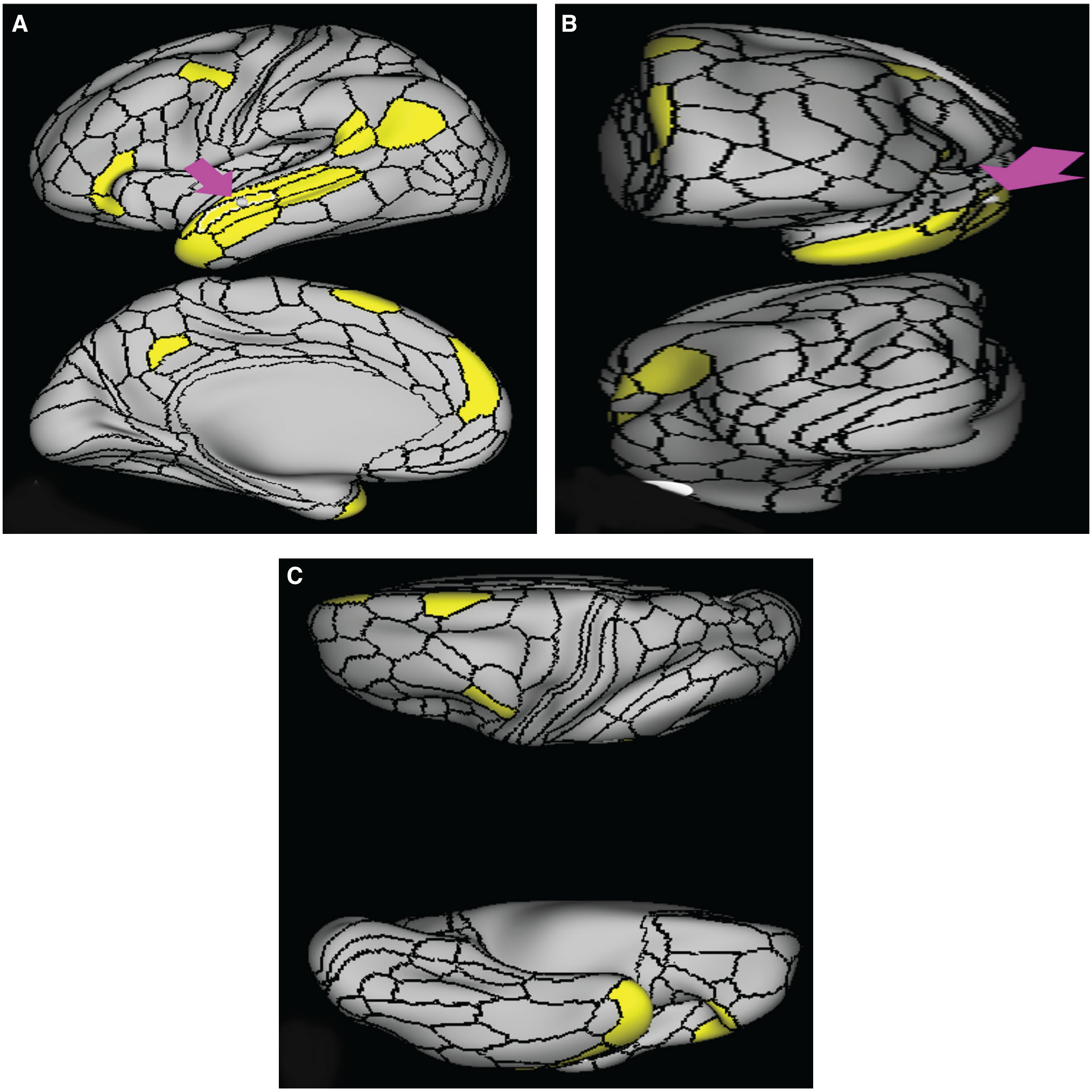

FIGURE 3. *Functional connectivity of STSda demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation of interest.*

of the occipitotemporal system. In some individuals, the STSda may also connect to the superior temporal terminations of inferior longitudinal fasciculus (ILF), though this is inconsistent across individuals and difficult to distinguish from the superior tracts of the MdLF. Arcuate/SLF tracts wrap around the Sylvian fissure projecting toward the frontal lobe and turn medially to terminate at FOP1, FOP3, and FOP4. MdLF tracts project through the temporal lobe to end at V1, V2, V3, and V4. Local short association fibers include "u" fibers of the occipitotemporal system that connect to TGd, STSva, and A5 (Figure 4).

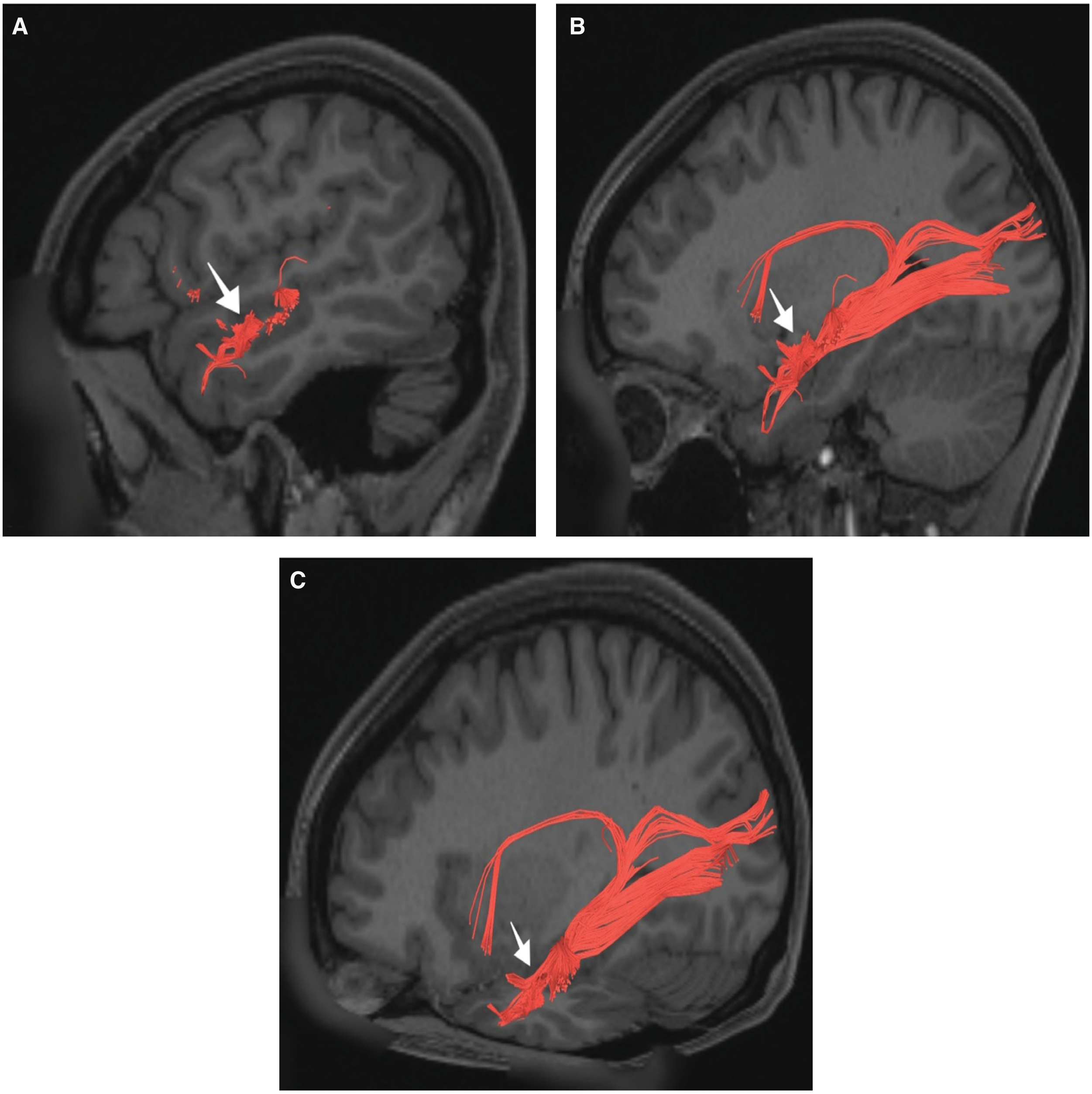

FIGURE 4. *Structural connectivity of STSda in the left hemisphere, shown on T1-weighted MR images.* **A-C**, *Three sagittal views from* **A**, *most lateral to* **B**, *and* **C**, *most medial showing projections to the frontal and occipital lobes. Red: white matter tracts of STSda demonstrating connections with arcuate/SLF, MdLF, and the "u" fibers of the occipito-temporal system.*

What is known about its function? The STS in general has been implicated in theory of mind along with the inferior temporal sulcus, medial prefrontal cortex, and temporal parietal junction.[1] The STS is also involved in motion processing, speech processing, and facial processing.[2] In addition to activating with unimodal visual and auditory inputs, the STS exhibits even stronger activation with combined audio and visual stimuli indicating a role in audiovisual integration.[2] Based on activations during tasks involved with semantic processing of auditory inputs, STSda, STSva, STSdp, and STSvp may be categorized as belonging to an auditory association cortex with areas A4, A5, STGa, and TA2.[1]

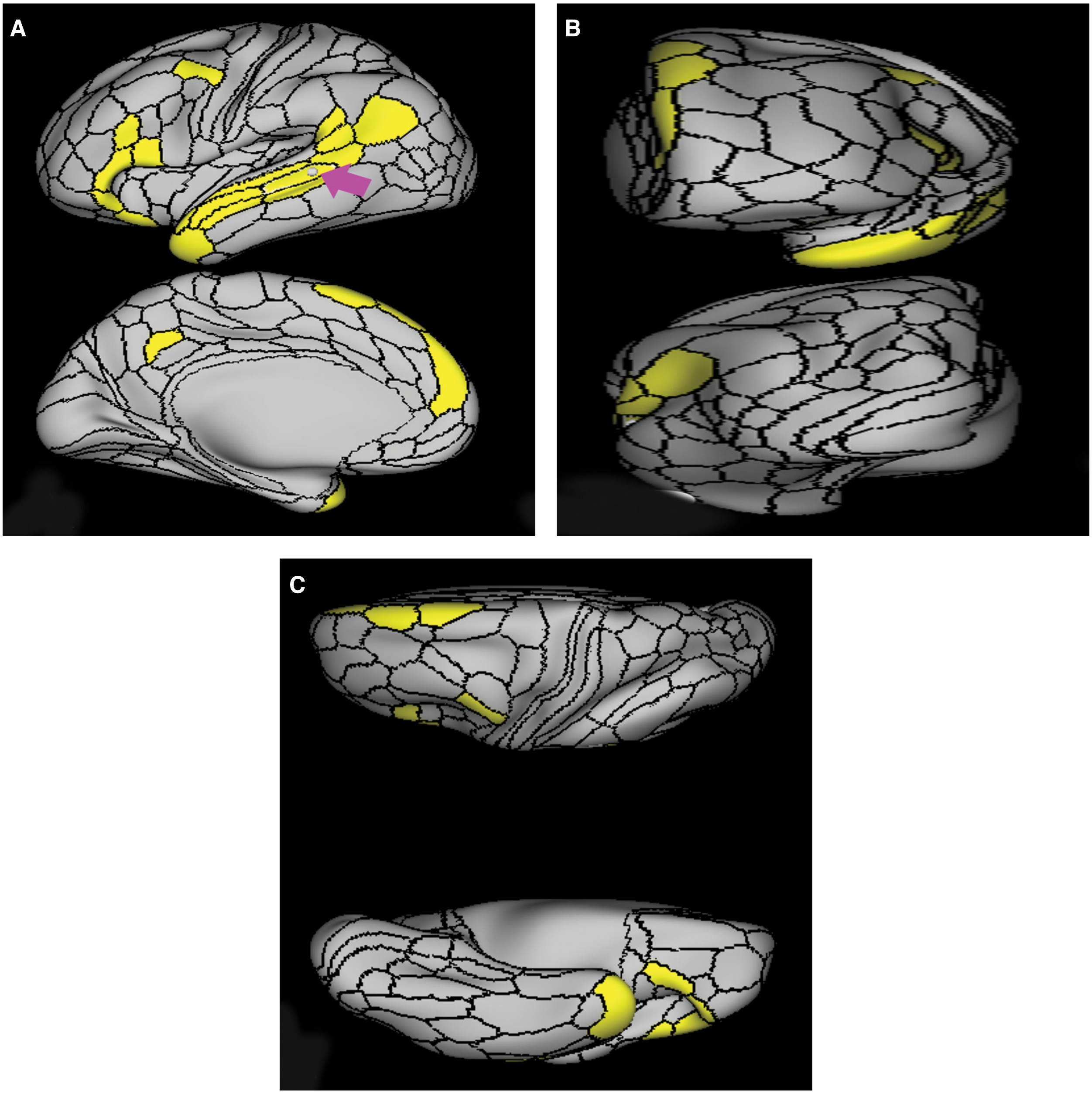

FIGURE 5. *Functional connectivity of STSdp demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation of interest.*

STSda, as part of the anterior portion of the STS, is primarily implicated in speech processing.[2] STSda is also activated in language-related task contrasts.[1] Relative to STSva inferiorly, STSda shows greater activation in motor tasks and less deactivation in tasks involving reward processing and decision making.[1]

Area STSdp

Where is it? Area STSdp is found on the posterior half of the lateral face of the STG and the posterior half of the superior bank of the STS.

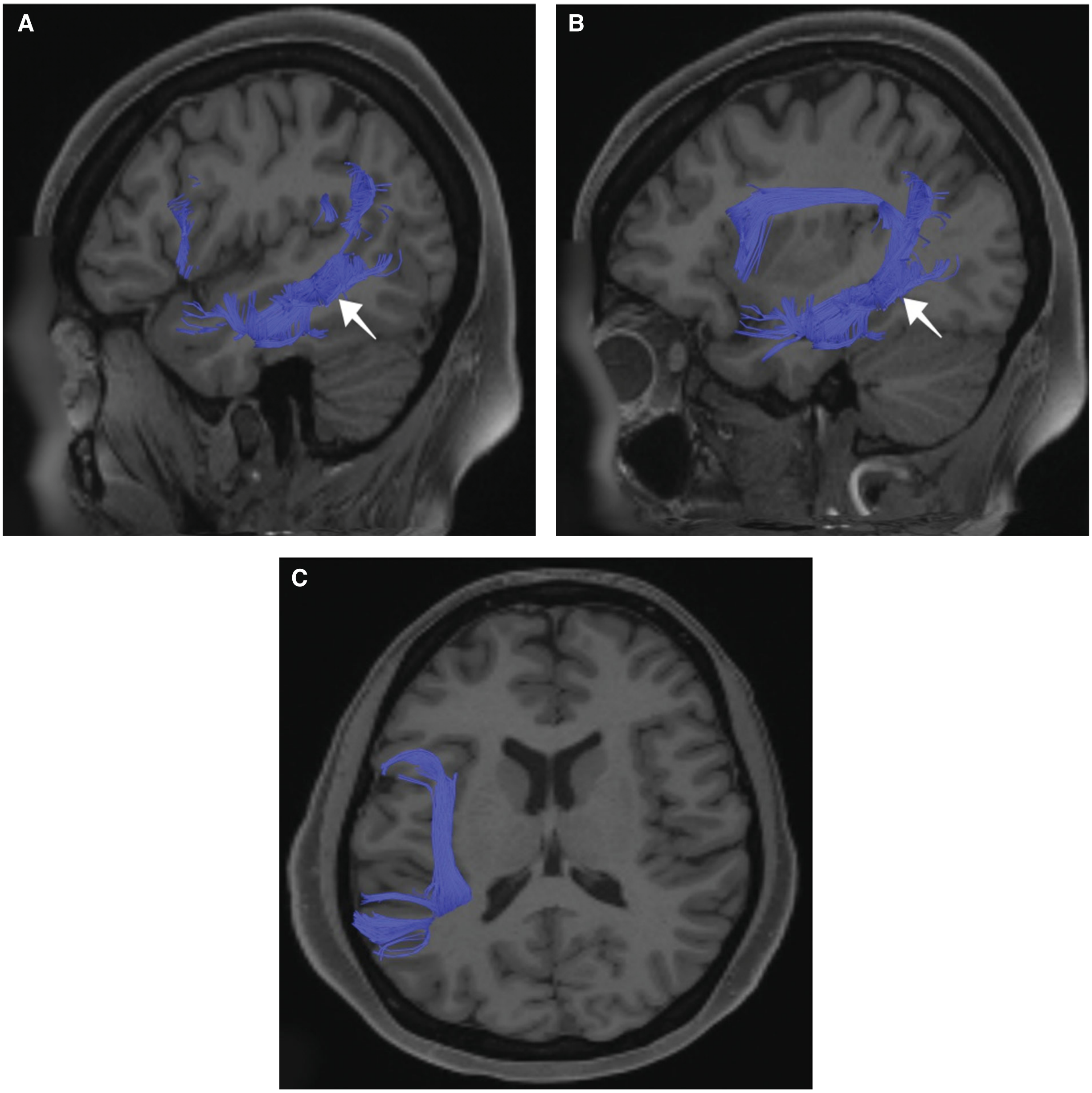

FIGURE 6. *Structural connectivity of STSdp in the left hemisphere, shown on T1-weighted MR images. Sagittal views of* **A**, *lateral and* **B**, *medial planes and* **C**, *axial views showing projections to the frontal and occipital lobes. Dark blue: white matter tracts of STSdp demonstrating connections with arcuate/SLF and the "u" fibers of the occipitotemporal system.*

What are its borders? Area STSdp borders area STSda anteriorly, STSvp inferiorly, TPOJ1 posteriorly, and A5 superiorly.

What is its functional connectivity? Area STSdp demonstrates functional connectivity to areas 9m, 8BL, 44 45, 47L, 47s, IFSp, SFL, and 55b in the frontal lobe, areas STV, PSL, A5, and STGa in the insula opercular area, areas STSva, STSvp, STSda, and TGd in the temporal lobe, TPOJ1 in the lateral occipital lobe, and PGi and 31pd in the parietal lobe (Figure 5).

What are its white matter connections? Area STSdp is structurally connected to the "u" fibers of the occipitotemporal system and the arcuate/SLF. Arcuate/SLF tracts wrap around

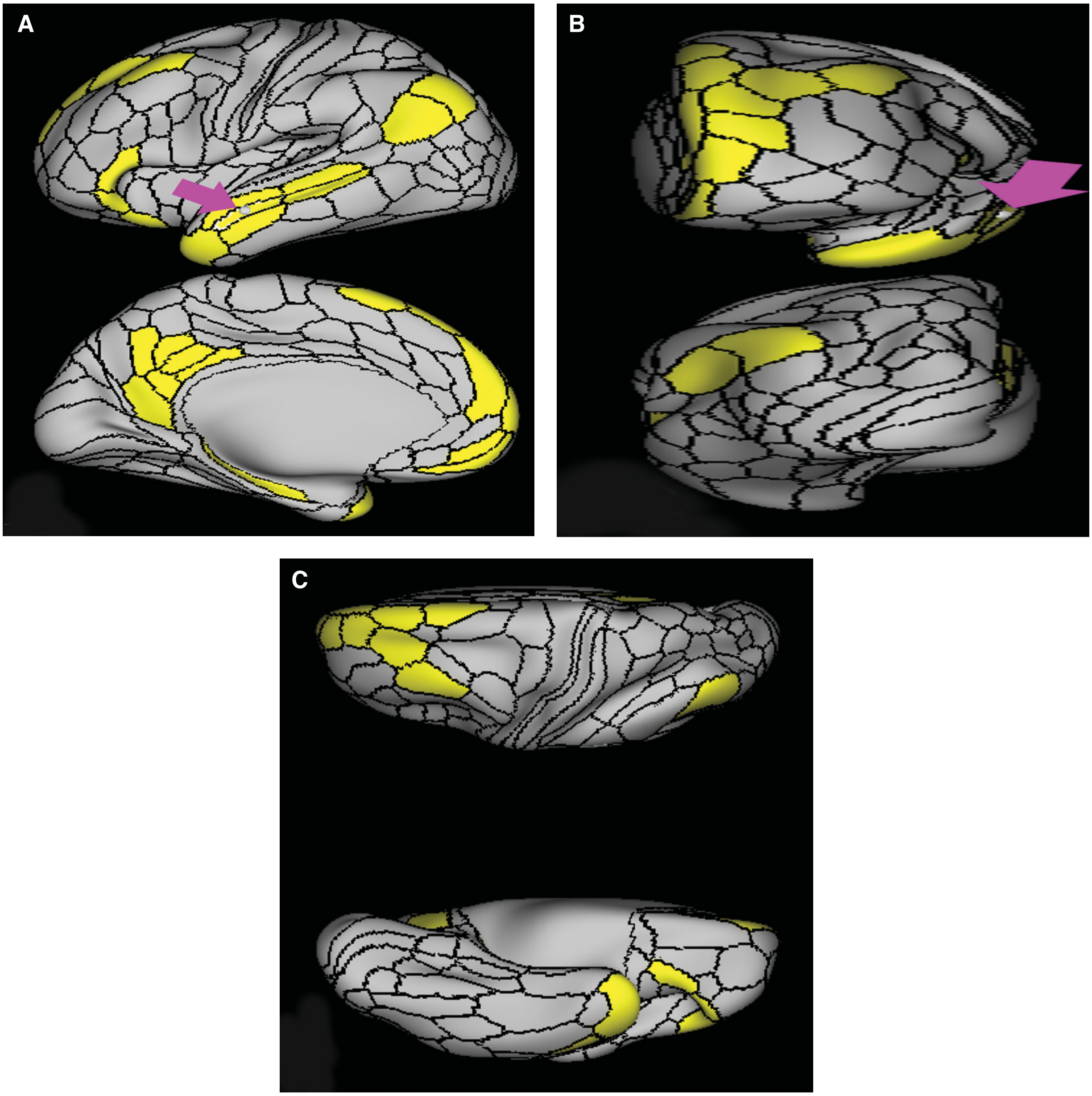

FIGURE 7. *Functional connectivity of STSva demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation of interest.*

the Sylvian fissure projecting toward the frontal lobe and turn medially to terminate at 44, FOP4, IFJa, IFJp, and IFSp. Local short association fibers include "u" fibers of the occipitotemporal system that connect to STSda, STSva, STSvp, PSL, and PF (Figure 6).

What is known about its function? The posterior portion of the STS is primarily involved in motion processing, audiovisual integration, and facial processing.[2] The posterior half of STSdp (like the posterior half of STSvp) is strongly activated in the story-math secondary contrast, indicating a role in language comprehension.[1] STSdp responds more strongly than STSvp to primary language tasks and to social cognition and motor tasks.[1]

Area STSva

Where is it? Area STSva is found on the anterior half of the inferior bank of the STS.

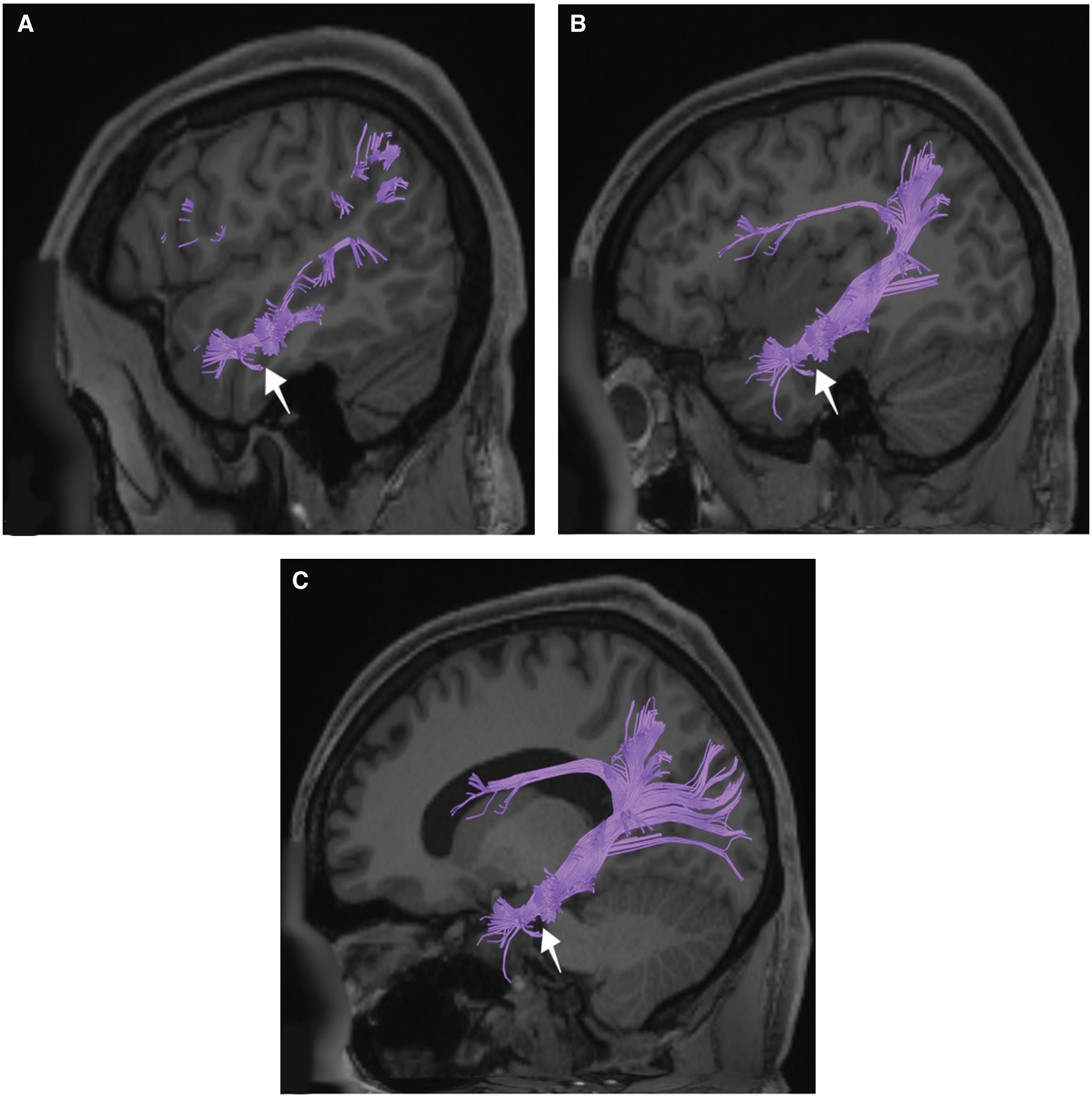

FIGURE 8. *Structural connectivity of STSva in the left hemisphere, shown on T1-weighted MR images.* **A** *to* **C***, Three sagittal views from* **A***, most lateral to* **B***, and* **C***, most medial showing projections to the frontal and occipital lobes. Purple: white matter tracts of STSva demonstrating connections with the arcuate/SLF, MdLF, the "u" fibers of the occipito-temporal system.*

What are its borders? Area STSva borders area STSvp posteriorly, TGd anteriorly, TE1a inferiorly, and STSda superiorly.

What is its functional connectivity? Area STSva is connected to 8AV, 8BL, 8AD, 9a, 9p, 9m, 45, 47s, 47L, 10d, 10r, 10v, and SFL in the frontal lobe, areas STSda, STSvp, STSdp, TGd, the hippocampus, and TE1a in the temporal lobe, and areas PGi, 7m, d23ab, 23d, 31pv, and 31pd in the parietal lobe (Figure 7).

What are its white matter connections? Area STSva is structurally connected to the MdLF, "u" fibers of the occipitotemporal system and the arcuate/SLF. Arcuate/SLF tracts wrap around the Sylvian fissure projecting toward the frontal lobe and turn medially to terminate at 44, IFJa, 6r, and 43. MdLF fibers course through the temporal lobe to end at V1, V2, V3, V4, and V3a. This tract may involve superior portions of the ILF. Local short association fibers include "u" fibers of the

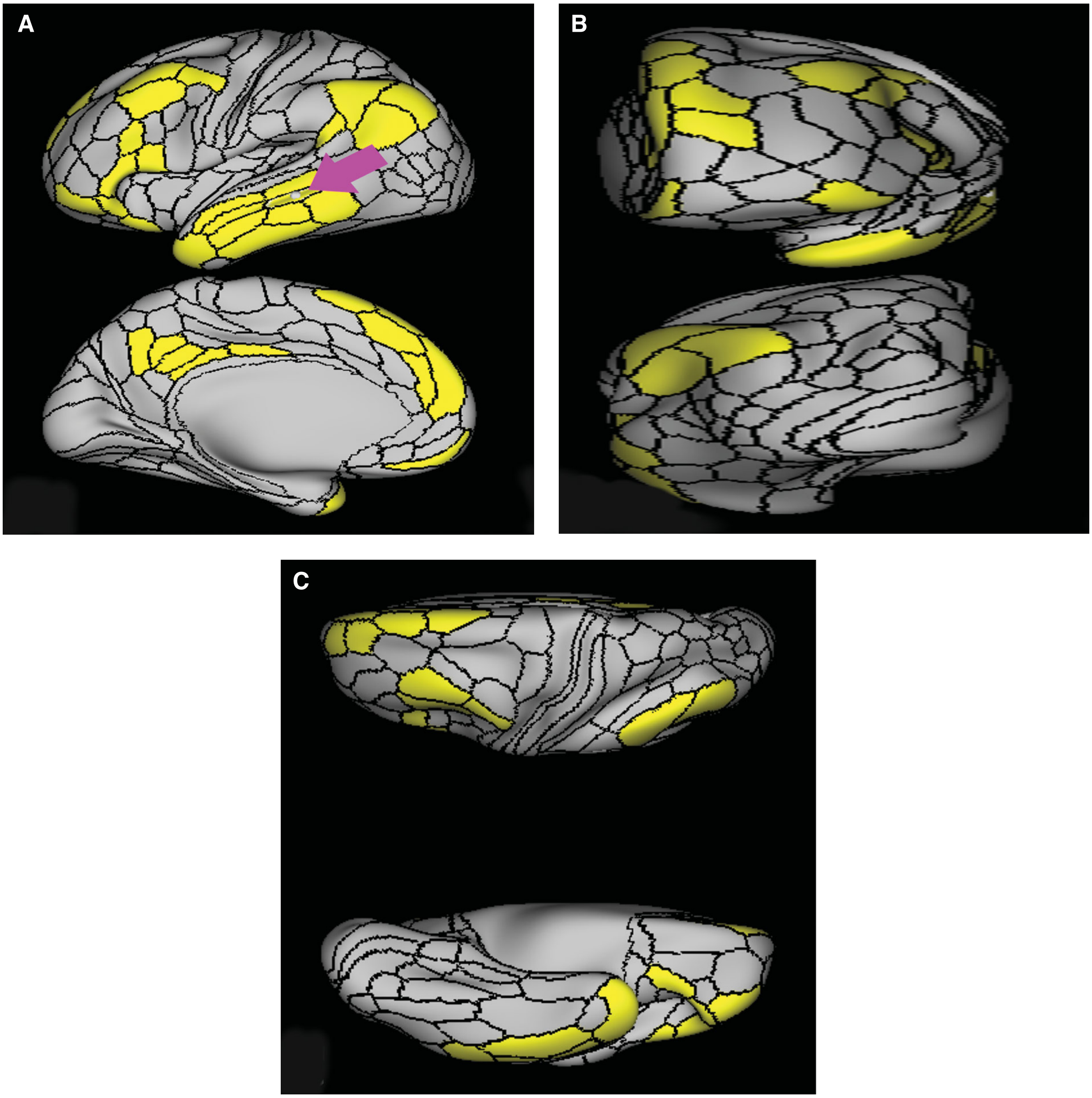

FIGURE 9. *Functional connectivity of STSvp demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation of interest.*

occipitotemporal system that connect to STSda, STSdp, STSvp, PSL, PFm, and PF (Figure 8).

What is known about its function? As part of the anterior portion of the STS, STSva is primarily implicated in speech processing.[2] STSda is activated in the story-math contrast as well as in primary language tasks.[1] Relative to STSda inferiorly, STSva is less activated in motor tasks and more deactivated in tasks involved with reward processing and decision making.[1]

Area STSvp

Where is it? Area STSvp is found on the posterior half of the inferior bank of the STS.

What are its borders? Area STSvp borders area STSva anteriorly, TE1m and temporal area 1 posterior (TE1p) inferiorly, TPOJ1 and PHT posteriorly, and STSdp superiorly.

What is its functional connectivity? Area STSvp demonstrates functional connectivity to 8AV, 8BL, 8BM, 8C, 9a, 9p, 9m, 44,

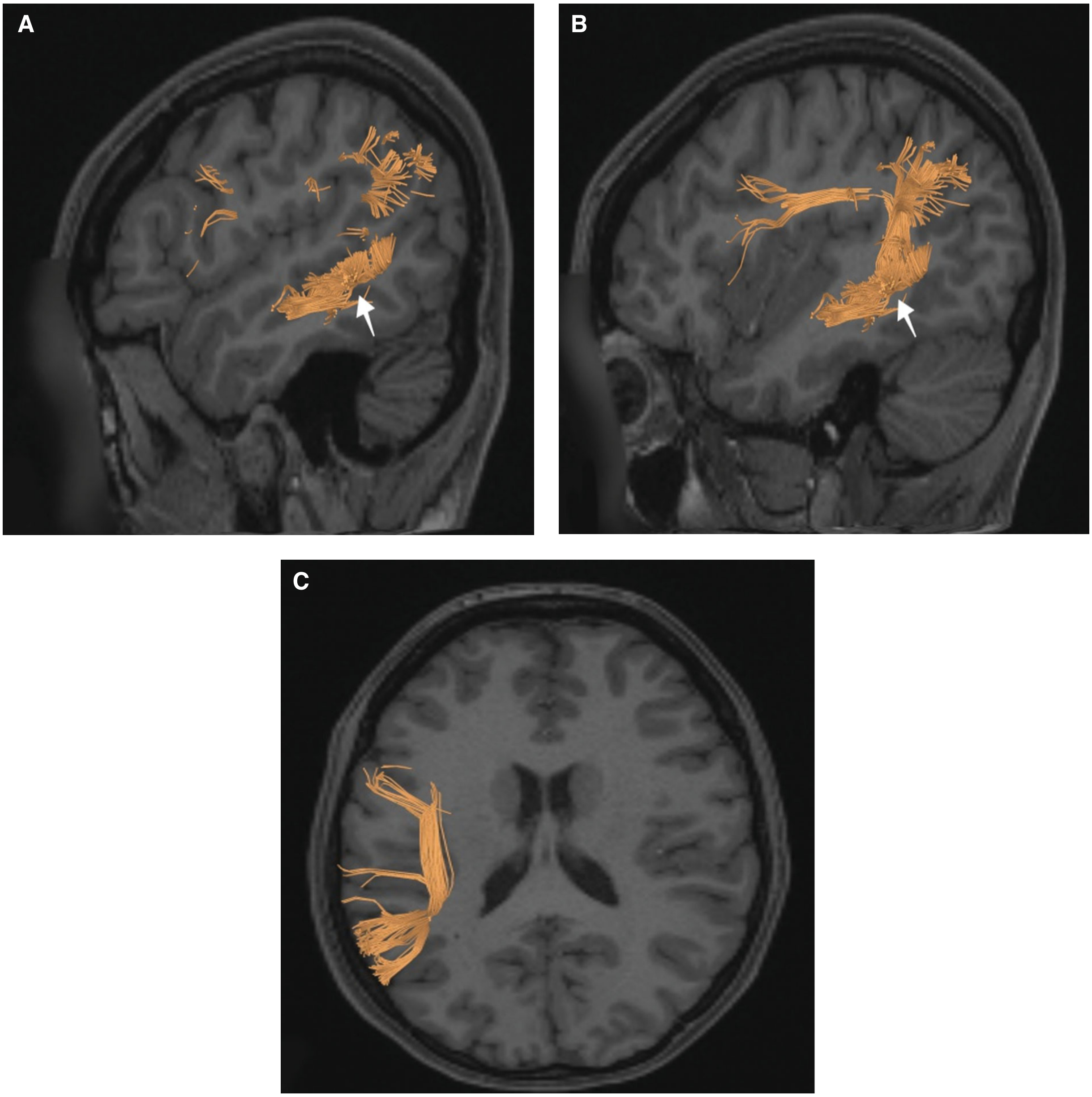

FIGURE 10. *Structural connectivity of STSvp in the left hemisphere, shown on T1-weighted MR images. Sagittal views of* **A**, *lateral and* **B**, *medial planes and* **C**, *axial views showing projections to the frontal and occipital lobes, and Inferior Parietal Lobule. Light orange: white matter tracts of STSvp projecting to the arcuate/SLF and the "u" fibers of the occipito-temporal system.*

45, 47s, 47L a47r, IFSp, d32, 10v, SFL, and 55b in the frontal lobe, area PSL in the insula opercular area, areas STSva, STSda, STSdp, TGd, temporal area 1 anterior (TE1a), TE1m, TE1p, and temporal area 2 anterior (TE2a) in the temporal lobe, and areas PGs, PGi, 7m, POS1, d23ab, 31pv, and 31pd in the parietal lobe (Figure 9).

What are its white matter connections? Area STSvp is structurally connected to "u" fibers of the occipito-temporal system and the arcuate/SLF. Arcuate/SLF tracts wrap around the Sylvian fissure projecting toward the frontal lobe to turn medially and terminate at 6r, IFJp, IFJa, FOP2, FOP3, FOP4, and 44. There are posterior projections from the arcuate/SLF as it wraps around the Sylvian fissure to terminate at the inferior parietal lobule

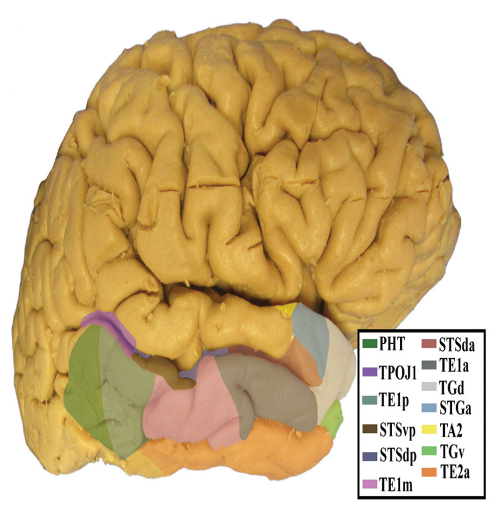

FIGURE 11. *Anatomic view of the TE1 parcellations shown on the right hemisphere of a cadaver brain.*

at PF, PFm, PSL, PGi, and STV. Local short association fibers include "u" fibers of the occipitotemporal system that connect to STSdp, STSva, TE1p, TE1m, PF, PFm, PSL, PGi, and STV (Figure 10).

What is known about its function? The posterior half of STSvp (like the posterior half of STSdp) is strongly activated by the story-math secondary contrast, indicating a role in language comprehension.[1] STSvp does not respond as strongly as STSva to primary language tasks, and is less active in social cognition and motor tasks.[1]

TE1 Areas

The anatomic locations of the pacellations that comprise the TE1 areas are shown in Figure 11. The parcellations include TE1a, temporal area 1 middle (TE1m), TE1p, and PHT. The combined tractography of the parcellations is shown in Figure 12.

Area TE1a

Where is it? Area TE1a is found on the anterior third of the lateral face of the MTG up to the edge of the inferior temporal sulcus.

What are its borders? Area TE1a borders STSva superiorly, TGd anteriorly, TE2a inferiorly, and TE1m posteriorly.

What is its functional connectivity? Area TE1a demonstrates functional connectivity to 8AV, 8AD, 8BL, 9a, 9p, 9m, a24, 45, 47s, 47L, 10d, 10v, 10r, and SFL in the frontal lobe, areas STSva, STSvp, STSda, TGv, entorhinal cortex (EC), the hippocampus, and TE1m in the temporal lobe, and areas PGs, PGi, 7m, d23ab, 31pv, and 31pd in the parietal lobe (Figure 13).

What are its white matter connections? Area TE1a is structurally connected to the arcuate/SLF, "u" fibers of the occipitotemporal system and the ILF. Arcuate/SLF tracts wrap around the Sylvian fissure projecting toward the frontal lobe to turn medially and terminate at 44, FOP4, and FOP3. There are posterior projections from the arcuate/SLF as it wraps around the Sylvian fissure to terminate at the inferior parietal lobule at PFm, PF, PSL, and STV. The ILF courses through the inferior temporal lobe to terminate at V1 and V2. Local short association fibers include "u" fibers of the occipitotemporal system that connect to STSva, STSvp, and TE1m (Figure 14). White matter tracts of TE1a in the right hemisphere have more consistent connections with the MdLF.

What is known about its function? The inferior TE is thought to be the final stage of the ventral visual processing pathway, and therefore is likely responsible for processing and representing information about complex visual objects.[3] TE is also important for short term maintenance of visual object information as part of working memory.[3] Both TE1 and TE2 are thought to be primarily unimodal visual areas and not heavily involved with processing of audio or somatosensory inputs.[4]

TE1a appears to break this functional pattern found in the literature because it is more active in semantic pathways than visual pathways.[1] TE1a is deactivated rather than activated during tasks requiring recognition of relationships between visual objects, visual working memory tasks, and motor activity tasks.[1] In contrast, relative to TE1m, TE1a shows greater activation in language processing tasks.[1]

Area TE1m

Where is it? Area TE1m is found on the lateral surface of the middle portion of the MTG. It spills across the corresponding portion of the inferior temporal sulcus and occupies some of the superior portion of the corresponding portion of the ITG.

What are its borders? Area TE1m borders TE1a anteriorly and TE1p posteriorly. Its superior border is STSvp and its inferior border is TE2a.

What is its functional connectivity? Area TE1m demonstrates functional connectivity to a47r, 8AV 8BL, 8AD, 8C, 9p, 47L, i6-8, and s6-8 in the frontal lobe, areas STSvp, TE2a, TE1p, and TE1a in the temporal lobe, and areas PGs, PFm, IP1, 7m, d23ab, 31pv, and 31pd in the parietal lobe (Figure 15).

What are its white matter connections? Area TE1m is structurally connected to the arcuate/SLF and "u" fibers of the occipitotemporal system. Arcuate/SLF tracts wrap around the Sylvian fissure projecting toward the frontal lobe to turn medially and end at 44, 45, IFJa, IFJp, and 8C. There are posterior projections from the arcuate/SLF that terminate at the inferior parietal lobule

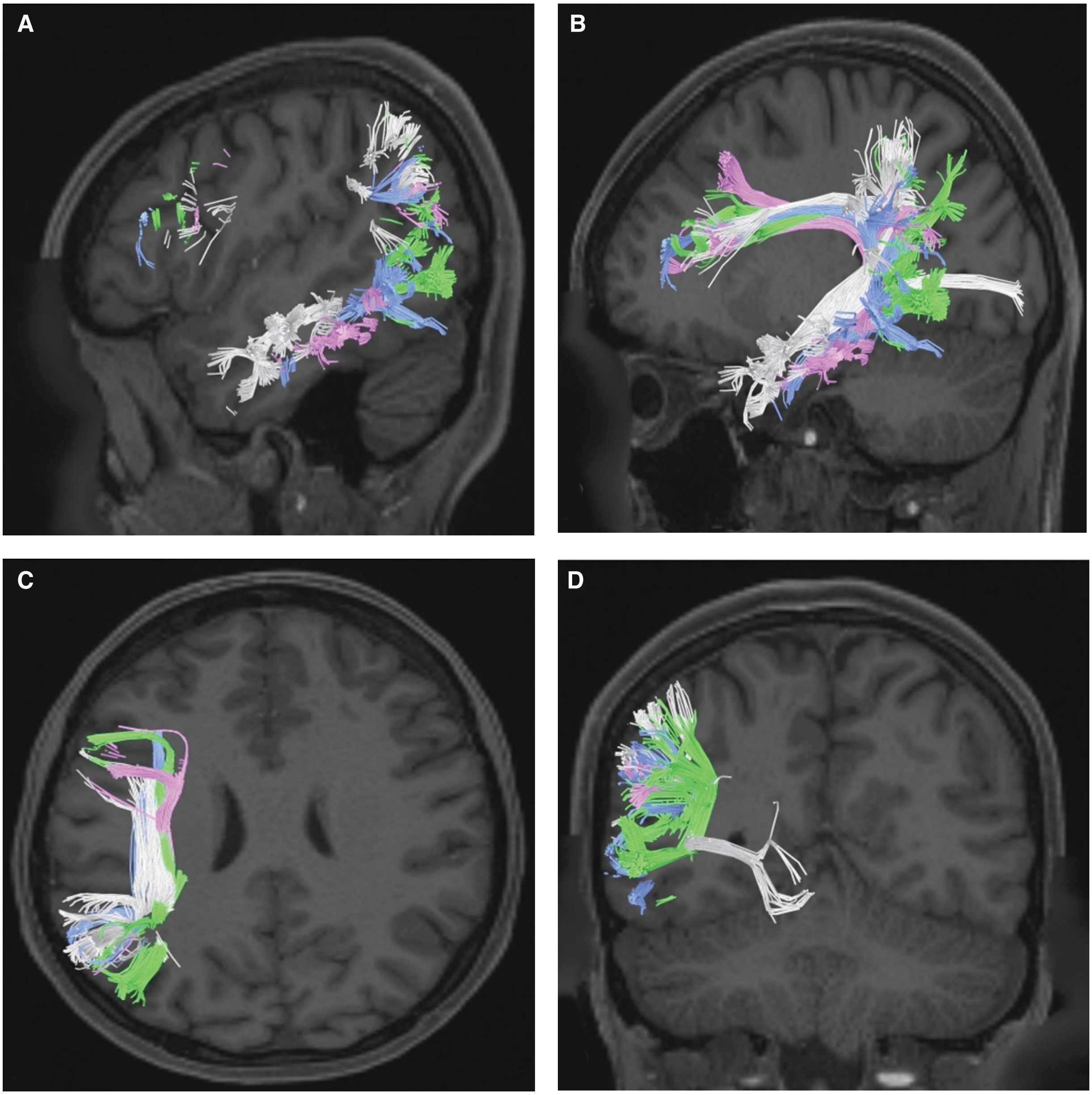

FIGURE 12. *Combined structural connectivity of the TE1 parcellations, shown on T1-weighted MR images. Sagittal views of* **A**, *lateral and* **B**, *medial planes.* **C**, *Axial view.* **D**, *Coronal view. Tracks correspond to TE1a (white), TE1m (pink), TE1p (blue), and PHT (light green).*

at PGi and PFm. Local short association fibers include "u" fibers of the occipitotemporal system that connect to TE1p and TE1a (Figure 16).

What is known about its function? The function of area TE1m appears primarily related to visual pathways.[1] TE1m, like TE1p, shows greater activation in the visual working memory secondary contrast compared to area TE1a.[1] Relative to TE1p, TE1m is less deactivated during language tasks and more deactivated in theory of mind tasks.[1] In fact, TE1m is more deactivated in theory of mind tasks than all of its neighbors.[1]

Area TE1p

Where is it? Area TE1p is found on the posterior most portions of the middle and inferior temporal gyri and the intervening inferior

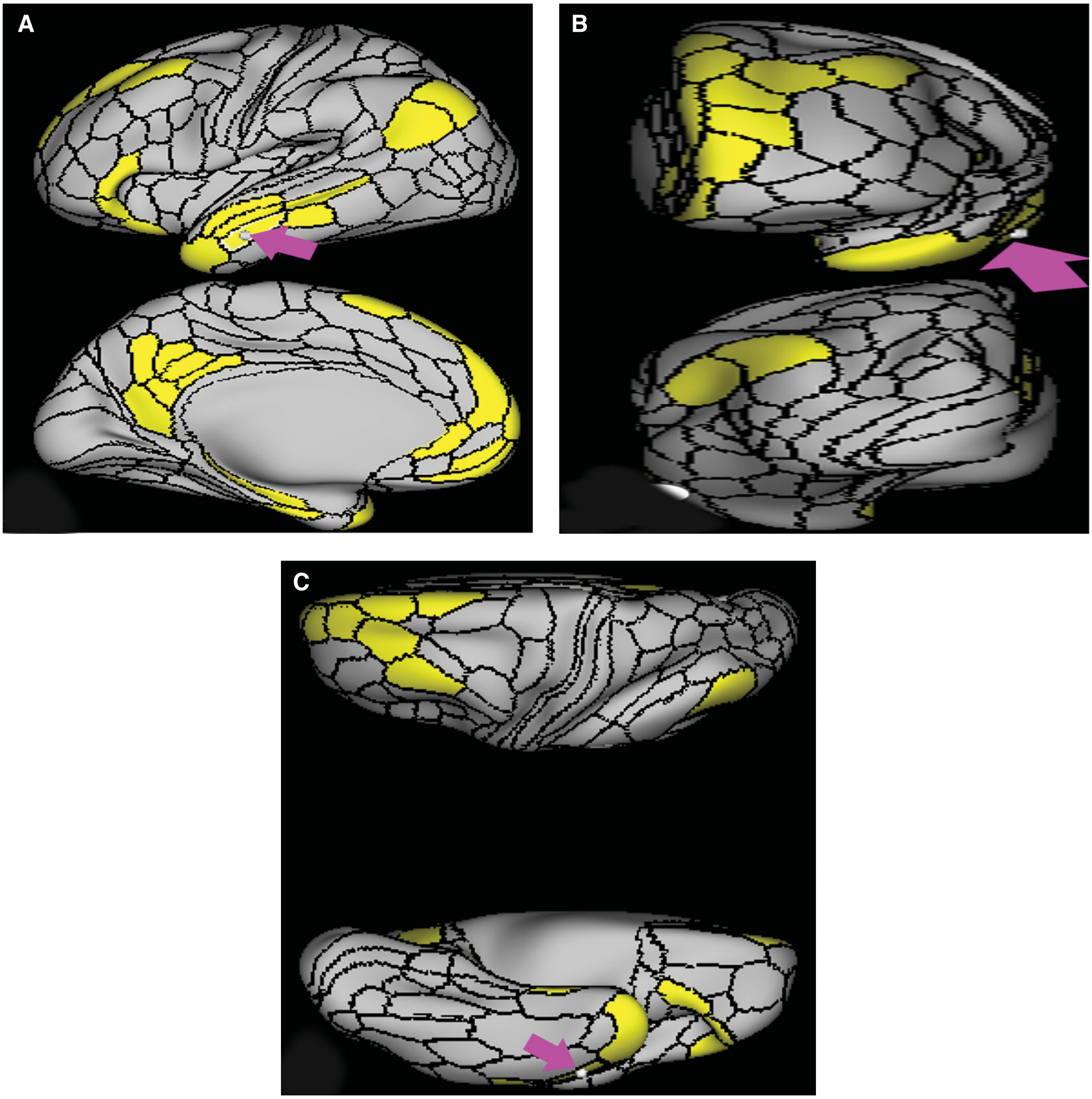

FIGURE 13. *Functional connectivity of TE1a demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation of interest.*

temporal sulcus. It spills onto the basal face of the temporal lobe and extends up to the occipitotemporal sulcus.

What are its borders? Area TE1p borders TE1m and TE2a anteriorly. Its posterior border is made up of PHT on the lateral surface and PH on the basal surface. Temporal area 2 posterior (TE2p) forms its inferobasal edge and STSvp forms its superior edge.

What is its functional connectivity? Area TE1p demonstrates functional connectivity to 33prime, 8AV, 8AD, 8BM, 8C, IFSa, IFSp, IFJp, a47r, p47r, 47m, a9-46v, p9-46v, i6-8, and s6-8 in the

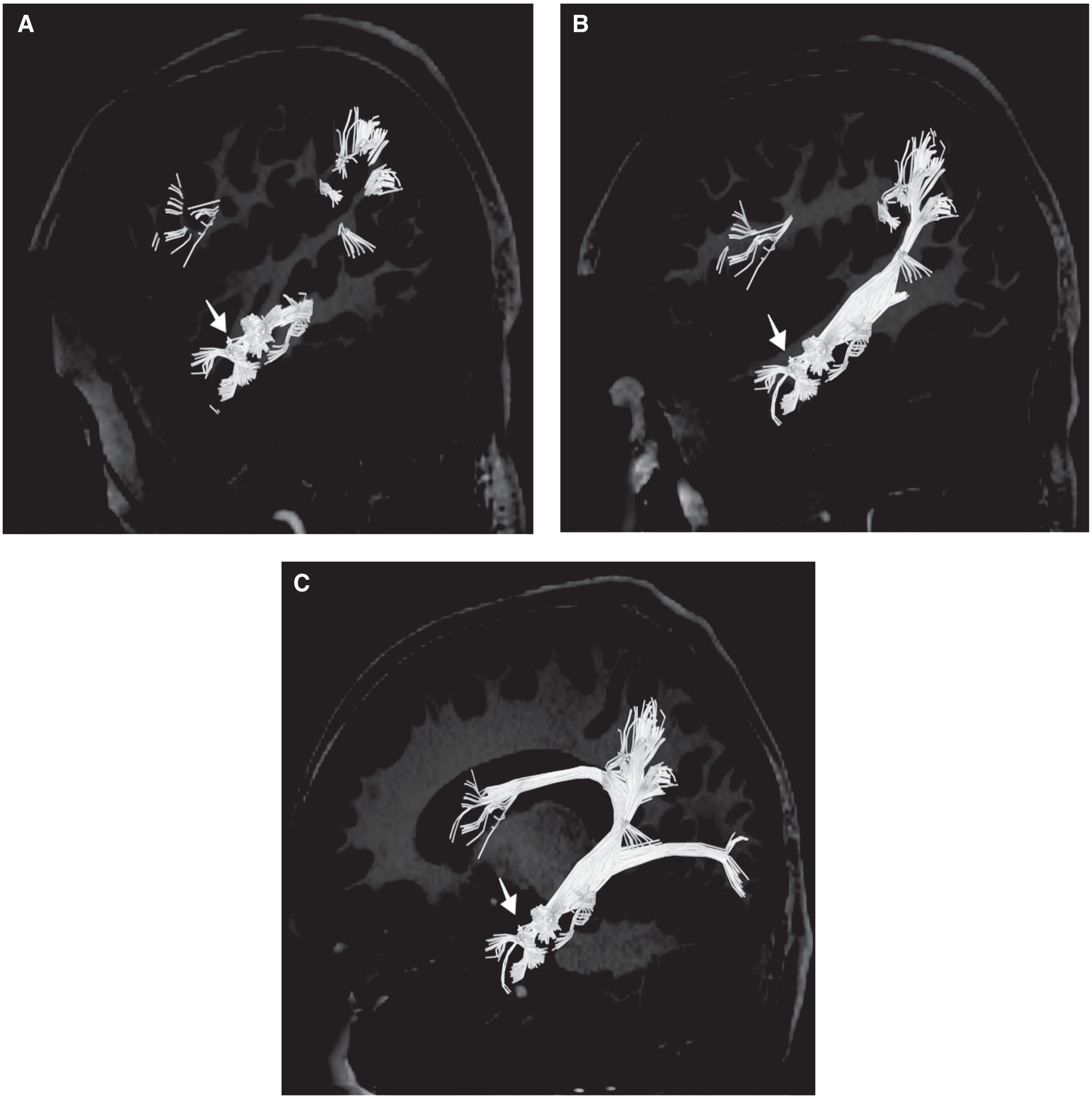

FIGURE 14. *Structural connectivity of TE1a in the left hemisphere, shown on T1-weighted MR images.* **A** *to* **C***, Three sagittal views from* **A***, most lateral to* **B** *and* **C***, most medial showing projections to the frontal and occipital lobes and inferior parietal lobule. White: white matter tracts of TE1a demonstrating connections with arcuate/SLF, the "u" fibers of the occipito-temporal system, and the ILF.*

frontal lobe, areas STSvp, PHT, TE1m, and TE2a in the temporal lobe, and areas PGs, PGi, PFm, IP2, IP1, IP0, 7pm, 7m, d23ab, and 31a in the parietal lobe (Figure 17).

What are its white matter connections? Area TE1p is structurally connected to the arcuate/SLF and "u" fibers of the occipitotemporal system. Arcuate/SLF tracts wrap around the Sylvian fissure projecting toward the frontal lobe to turn medially and end at 45. There are abundant posterior projections from the arcuate/SLF that terminate at the inferior parietal lobule at STV, PFm, PSL, PGi, TPOJ1, TPOJ2, and STV. Local short association fibers include "u" fibers of the occipitotemporal system that connect to TE2a and perirhinal ectorhinal cortex (PeEc; Figure 18).

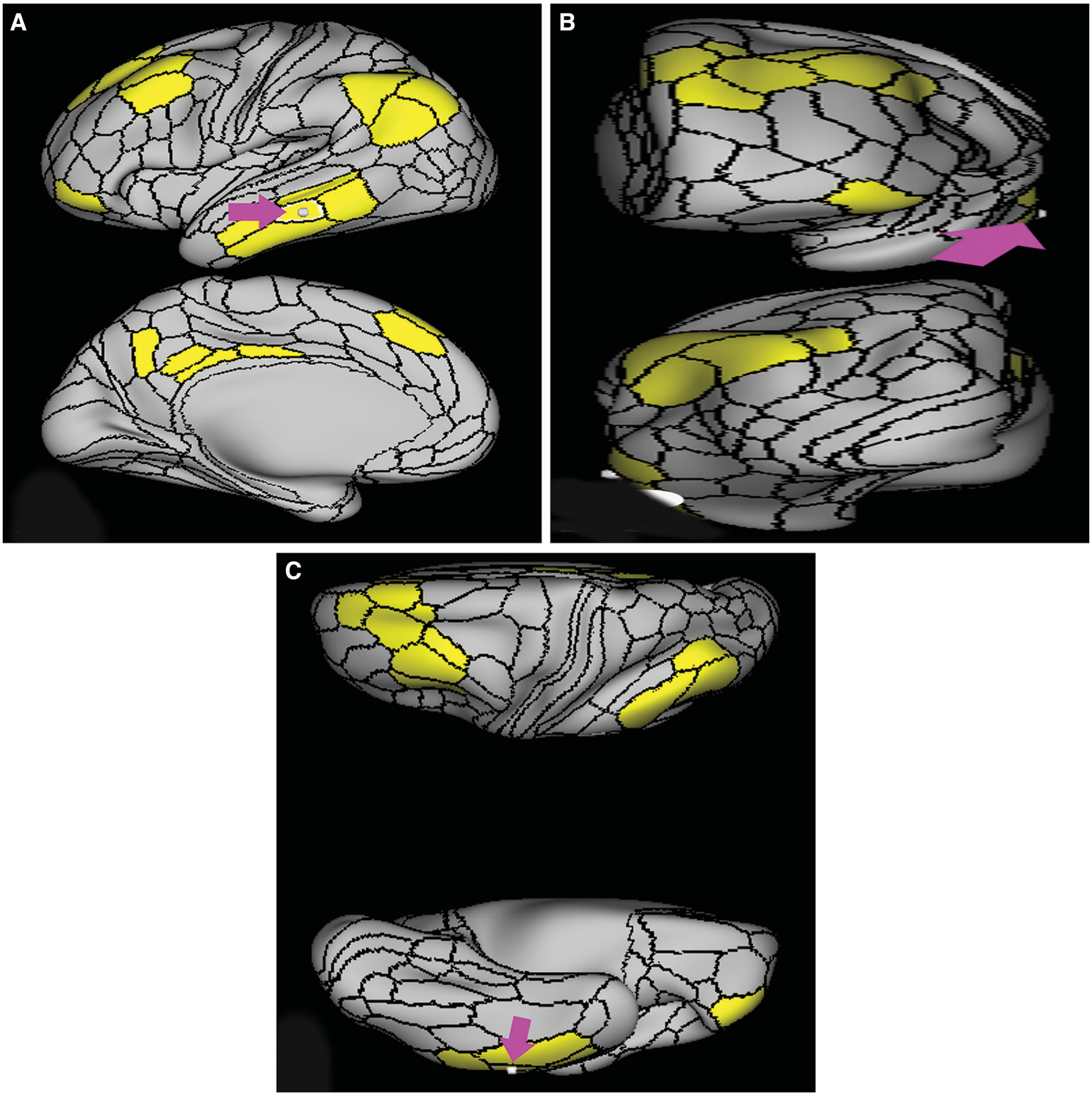

FIGURE 15. *Functional connectivity of TE1m demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation of interest.*

What is known about its function? The function of area TE1p appears primarily related to visual pathways.[1] TE1p, like TE1m, shows greater activation in the visual working memory secondary contrast compared to area TE1a.[1] Relative to TE1m, TE1p is more deactivated during language tasks and more activated during facial recognition tasks.[1]

Area PHT

Where is it? Area PHT is found on the anterior portions of the subcentral gyrus (where the precentral and postcentral gyri meet just below the central sulcus). It involves the lateral surface of that operculum as well as the inferior surface that faces the Sylvian Fissure.

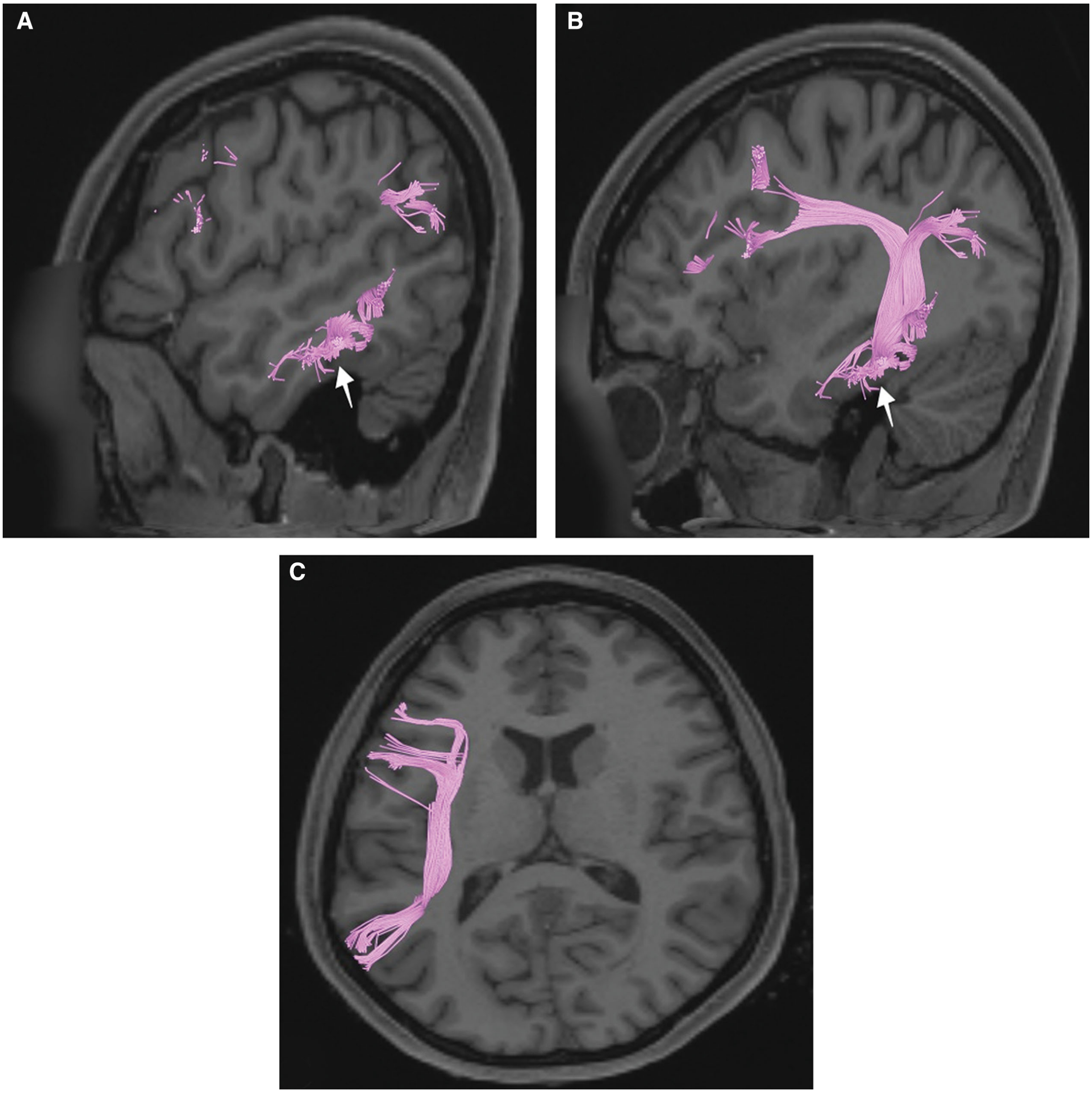

FIGURE 16. *Structural connectivity of TE1m in the left hemisphere, shown on T1-weighted MR images. Sagittal views of* **A**, *lateral and* **B**, *medial planes and* **C**, *axial views showing projections to frontal and occipital lobes and inferior parietal lobule. Light pink: white matter tracts of TE1m demonstrating connections with the arcuate/SLF and the "u" fibers of the occipito-temporal system.*

What are its borders? Area PHT borders area 6r anteriorly and OP4 posteriorly. Its superior border includes area 6v, as well as areas 4 and 3a. Its inferior borders include FOP1 and FOP2.

What is its functional connectivity? Area PHT demonstrates functional connectivity to areas IFSa, IFJa, IFJp, 6a, 6ma, 6r, 46, 9-46d, p9-46v, p47r, FEF, PEF, SCEF, a24prime, p24prime, p32prime, 33prime, 23c, and 5mv in the frontal lobe, areas FOP1, FOP3, FOP4, FOP5, 43, PFcm, 52, MI, PoI1, and PoI2 in the insula opercular area, areas TE1p, TE2p and parahippocampal area 3 (PHA3) in the temporal lobe, areas AIP, MIP, VIP, LIPv, LIPd, IPS1, IP0, IP1, IP2, PF, PFop, PFt, PGp, 7PC, 7pm, 7AL, 7PL, PCV, and DVT in the parietal lobe, and areas V1, V2, FST, PH, and TPOJ2 in the occipital lobe (Figure 19).

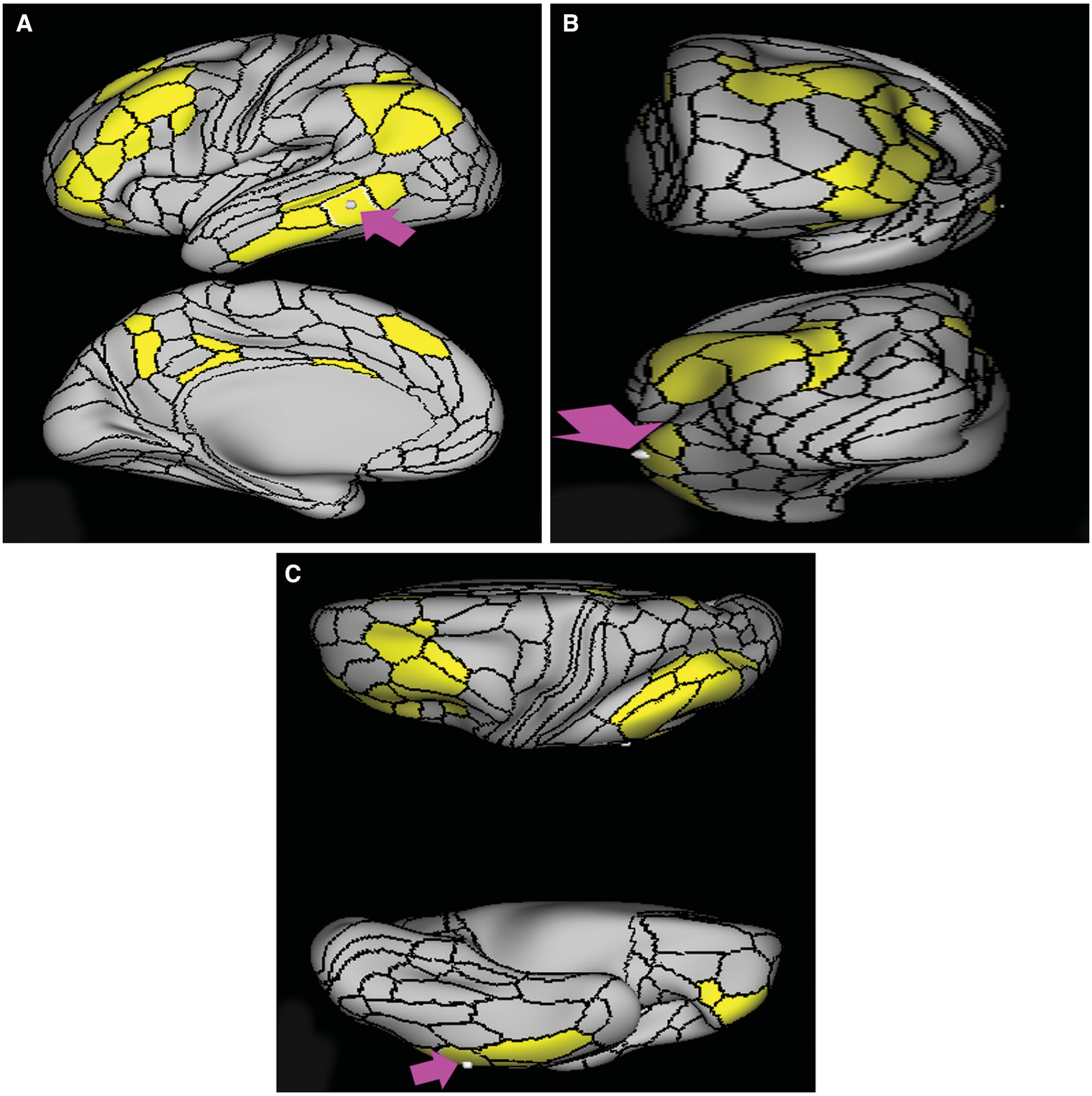

FIGURE 17. *Functional connectivity of TE1p demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation of interest.*

What are its white matter connections? Area PHT is structurally connected to the arcuate/SLF. Arcuate/SLF tracts wrap around the Sylvian fissure projecting toward the frontal lobe and turn medially to end at 44, IFJa, IFJp, and IFSp. There are abundant posterior projections from the arcuate/SLF that terminate at the inferior parietal lobule at PGs, STV, PFm, PGi, TPOJ1, and TPOJ2 (Figure 20).

What is known about its function? Area PHT lies in the posterior MTG leading into the angular gyrus. The posterior

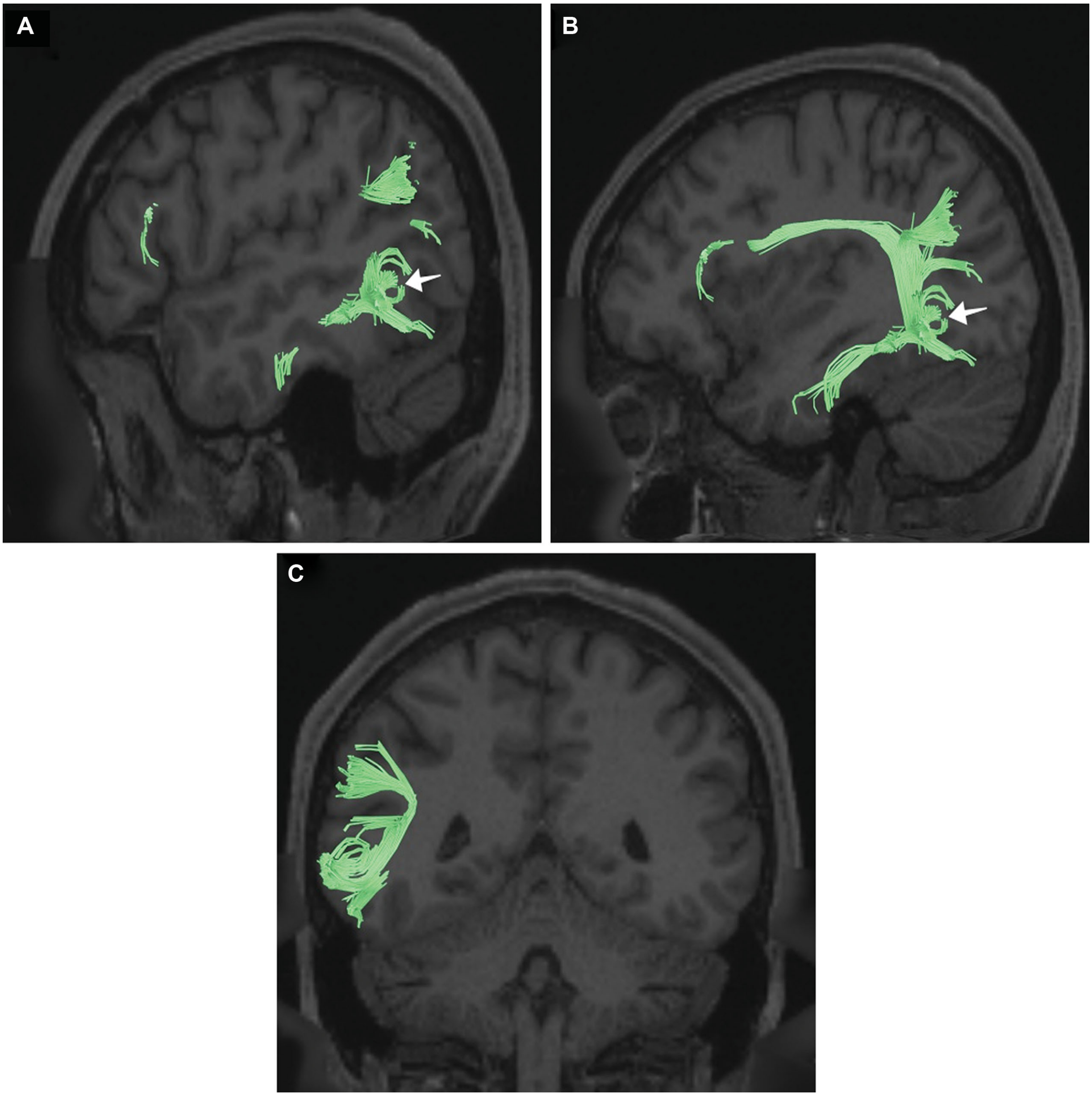

FIGURE 18. *Structural connectivity of TE1p in the left hemisphere, shown on T1-weighted MR images. Sagittal views of* **A**, *lateral and* **B**, *medial planes and* **C**, *coronal views showing projections to the frontal and occipital lobes and inferior parietal lobule. Light green: white matter tracts of TE1p demonstrating connections with the arcuate/SLF and the "u" fibers of the occipito-temporal system.*

MTG is involved in processes related to the controlled retrieval of conceptual knowledge, while the anterior gyrus is involved in the automatic retrieval of specific semantic information.[5] In contrast to the other parcellations of the lateral temporal cortex and temporal pole (TE1p, TE1m, TE1a, TE2p, TE2a, TGv, TGd, and TF) that are all strongly associated with the task negative network, PHT is strongly associated with the task positive network.[1] In addition, PHT (like TE1p anteriorly) is deactivated during language recognition tasks.[1]

TE2 and TF Areas

The anatomic locations of the parcellations that comprise the TE2 and TF areas are shown in Figure 21. The parcellations

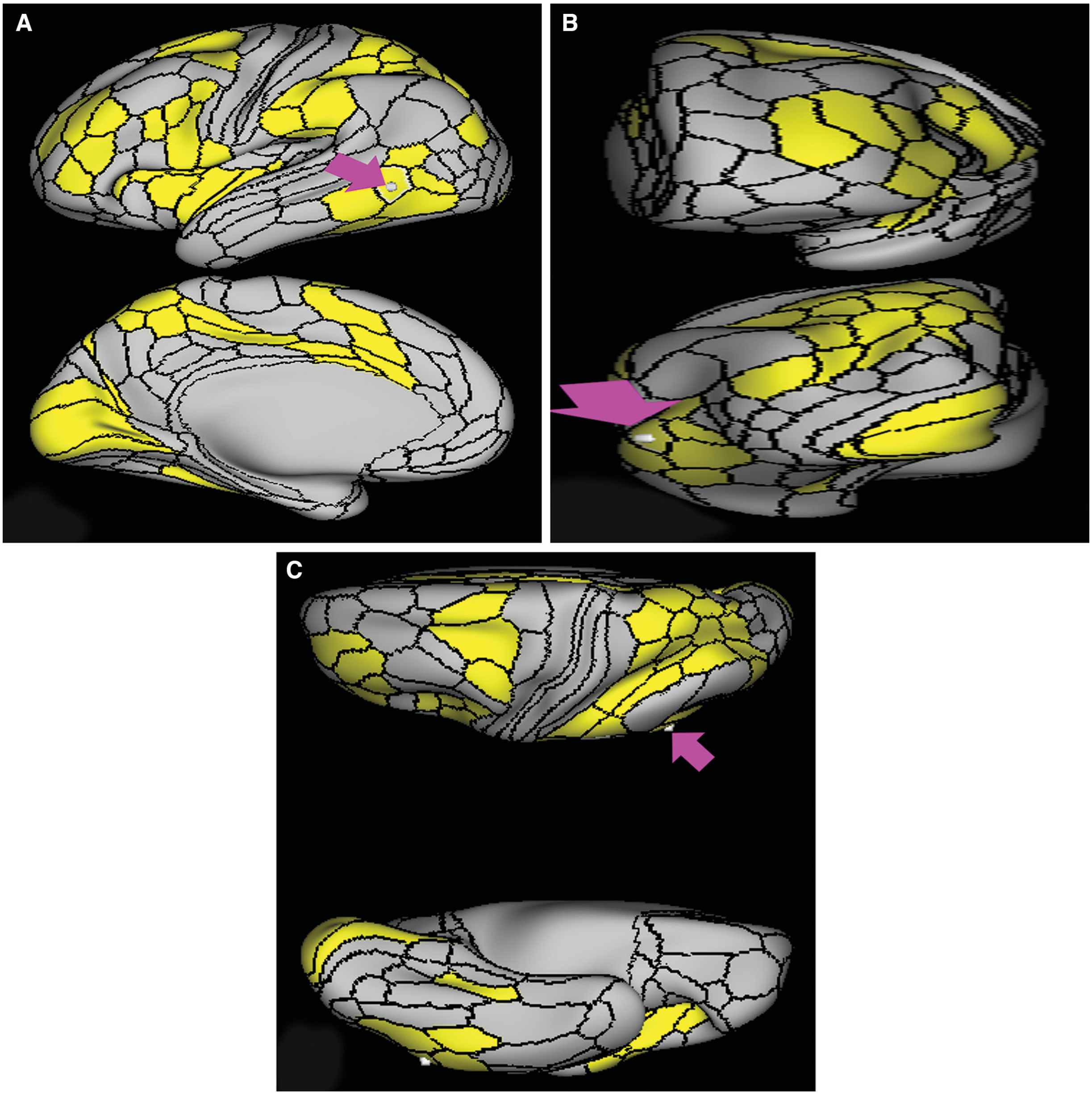

FIGURE 19. *Functional connectivity of PHT demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation of interest.*

include TE2a, TE2p, and TF. The combined tractography of the parcellations is shown in Figure 22.

Area TE2a

Where is it? Area TE2a is found on the anterior portion of the ITG, the anterior half of the inferior sulcus, and the lateral bank of the occipitotemporal sulcus.

What are its borders? Area TE2a borders TF on its basal-medial edge and TE1a and TE1m on its superior surface. It borders TGd and TGv anterior and its posterior end is wedged between TE1p and TE2p.

What is its functional connectivity? Area TE2a demonstrates functional connectivity to areas 8AV, 8BL, 8C, and a47r in the

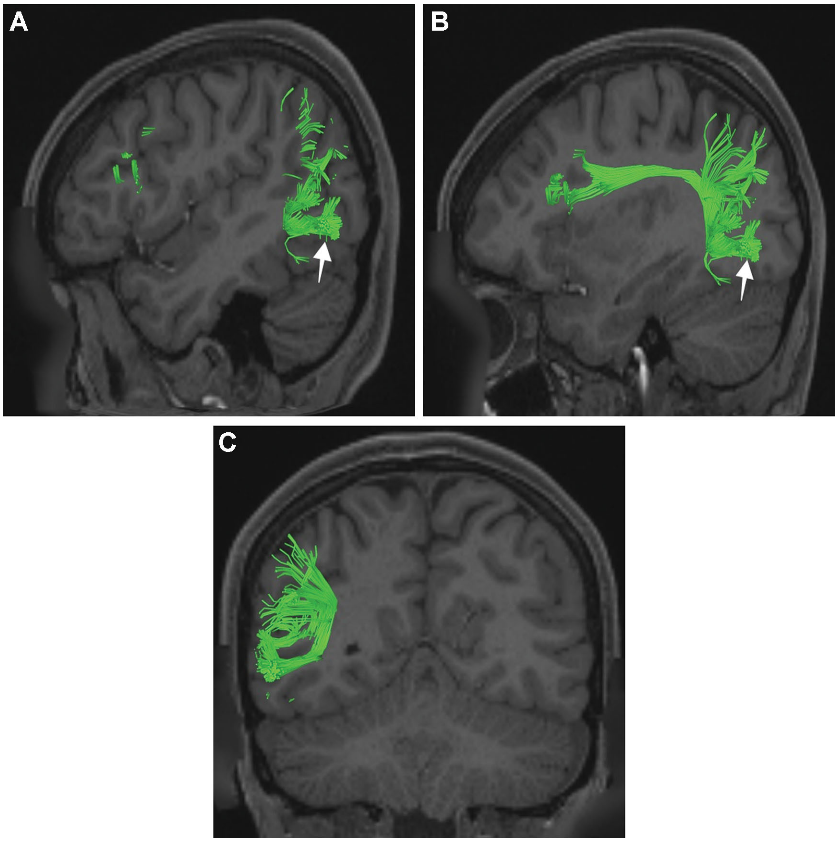

FIGURE 20. *Structural connectivity of PHT in the left hemisphere, shown on T1-weighted MR images. Sagittal views of* **A**, *lateral and* **B**, *medial planes and* **C**, *coronal views showing projections to the frontal and occipital lobe and inferior parietal lobule. Dark green: white matter tracts of PHT demonstrating connections with the arcuate/SLF and the "u" fibers of the occipitotemporal system.*

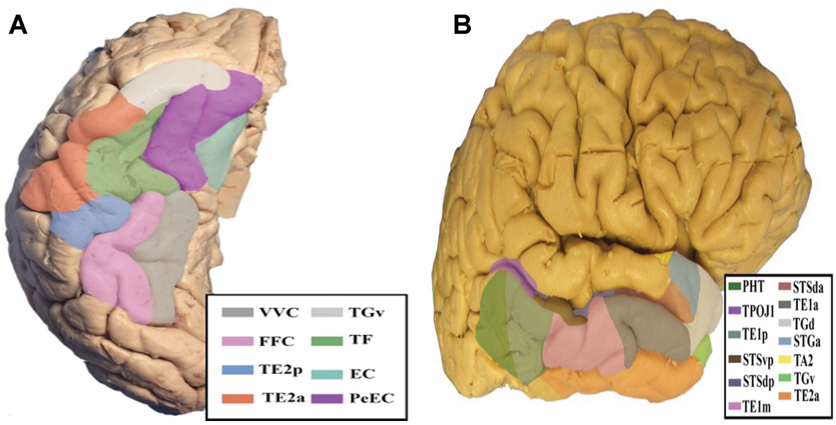

FIGURE 21. *Anatomic view of the TE2 and TF parcellations shown on the right hemisphere of a cadaver brain.* **A**, *Inferior view of the temporal lobe.* **B**, *Lateral view of temporal lobe.*

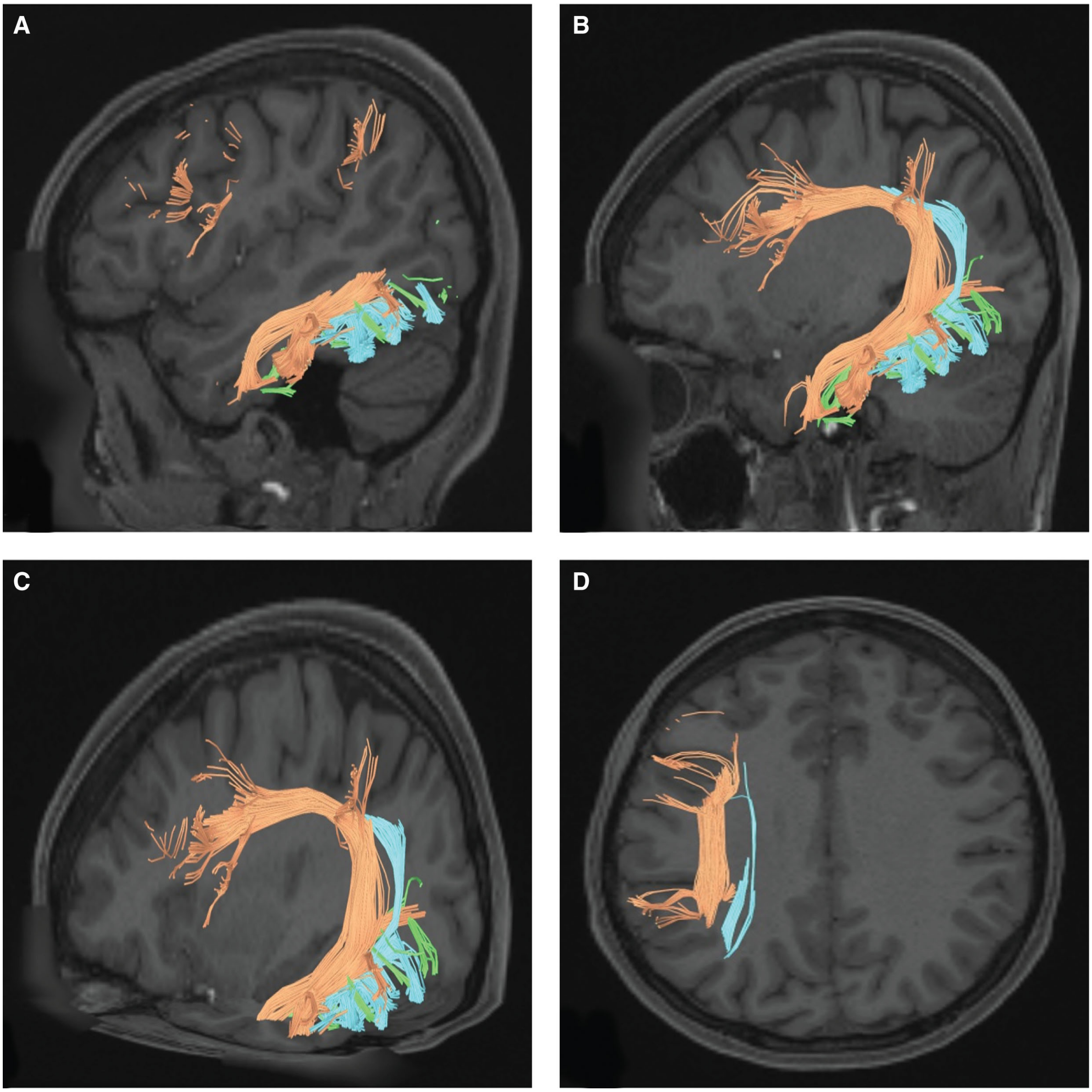

FIGURE 22. *Combined structural connectivity of the TE2 and TF parcellations, shown on T1-weighted MR images.* **A-C**, *Three sagittal views from* **A**, *most lateral to* **B** *and* **C**, *most medial.* **D**, *Axial view. Tracks correspond to TE2a (orange), TE2p (light blue), and TF (green)*

frontal lobe, areas STSvp, TE1m, and TE1p in the temporal lobe, and areas PGs, PGi, and PFm in the parietal lobe (Figure 23).

What are its white matter connections? Area TE2a is structurally connected to the arcuate/SLF and ILF. ILF projections are inconsistent across individuals. Arcuate/SLF tracts wrap around the Sylvian fissure projecting toward the frontal lobe and turn medially to terminate at 6r, 6v, 8C, p9-46v, IFJa, IFJp, and IFSp. There are posterior projections from the arcuate/SLF that terminate at the inferior parietal lobule at PF and PFm. Local short association fibers connect to TE1p and TGd Figure (Figure 24).

What is known about its function? The function of area TE2a appears primarily related to visual pathways.[1] TE2a has a similar functional profile to TE1m, which borders the region superiorly, including activation in the visual working memory secondary contrast and deactivation in language tasks.[1] Relative

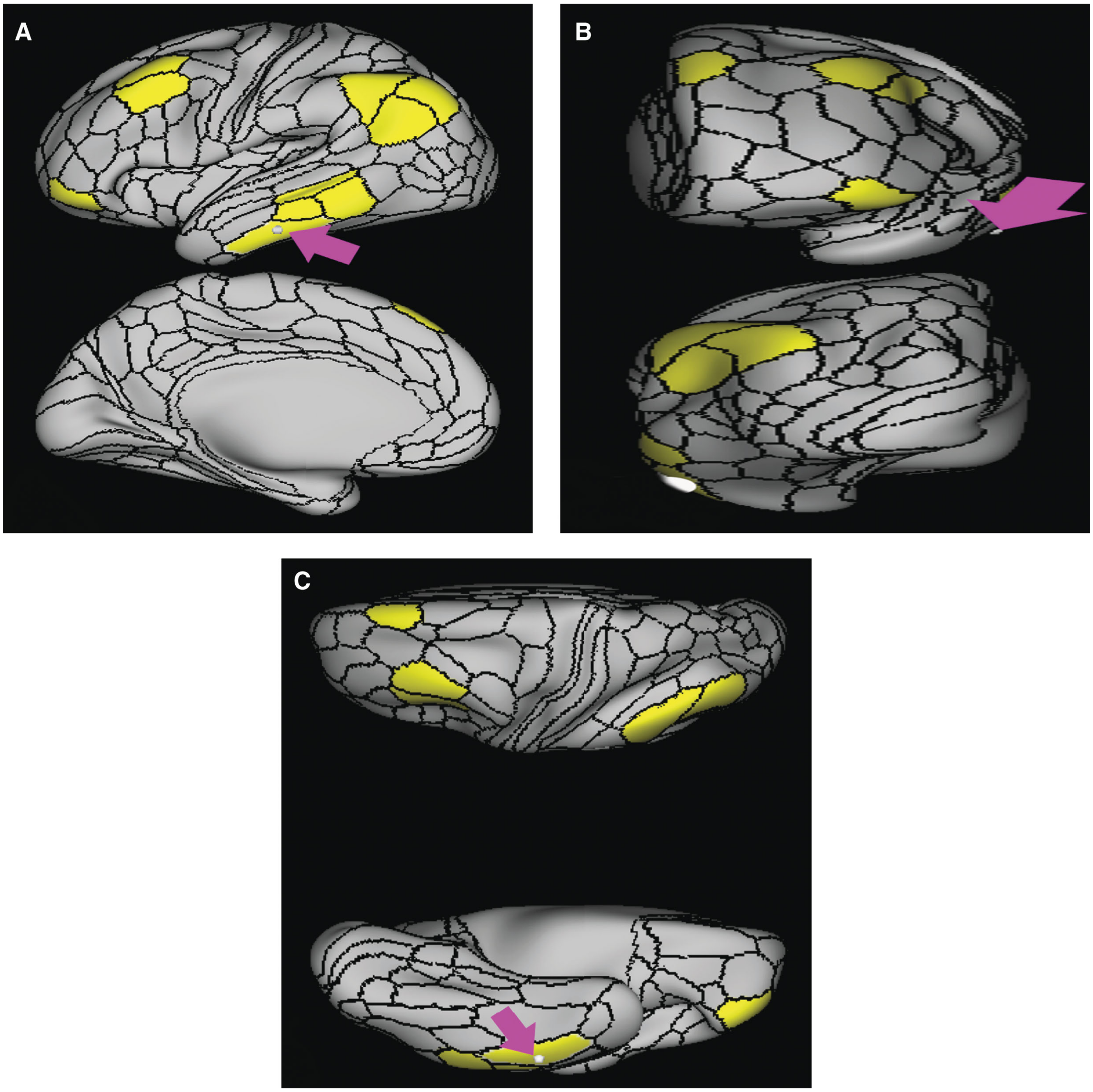

FIGURE 23. *Functional connectivity of TE2a demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation of interest.*

to TE1m, however, TE2a demonstrates less activation in visual working memory tasks and less deactivation during language tasks.[1]

Area TE2p

Where is it? Area TE2p is found in the posterior part of the occipital temporal sulcus and the middle posterolateral portion of the fusiform gyrus.

What are its borders? Area TE2p borders PH posteriorly, and FFC medially. Its anterior border is TF and its lateral border is made up of TE2a and TE1p.

What is its functional connectivity? Area TE2p demonstrates functional connectivity to areas FEF, PEF, IFSa, IFJa, IFJp, p9-46v, 6a, and 6r in the frontal lobe, area PoI2 in the insula, area PHT in the temporal lobe, areas PGp, AIP, MIP, LIPv, LIPd, IPS1,

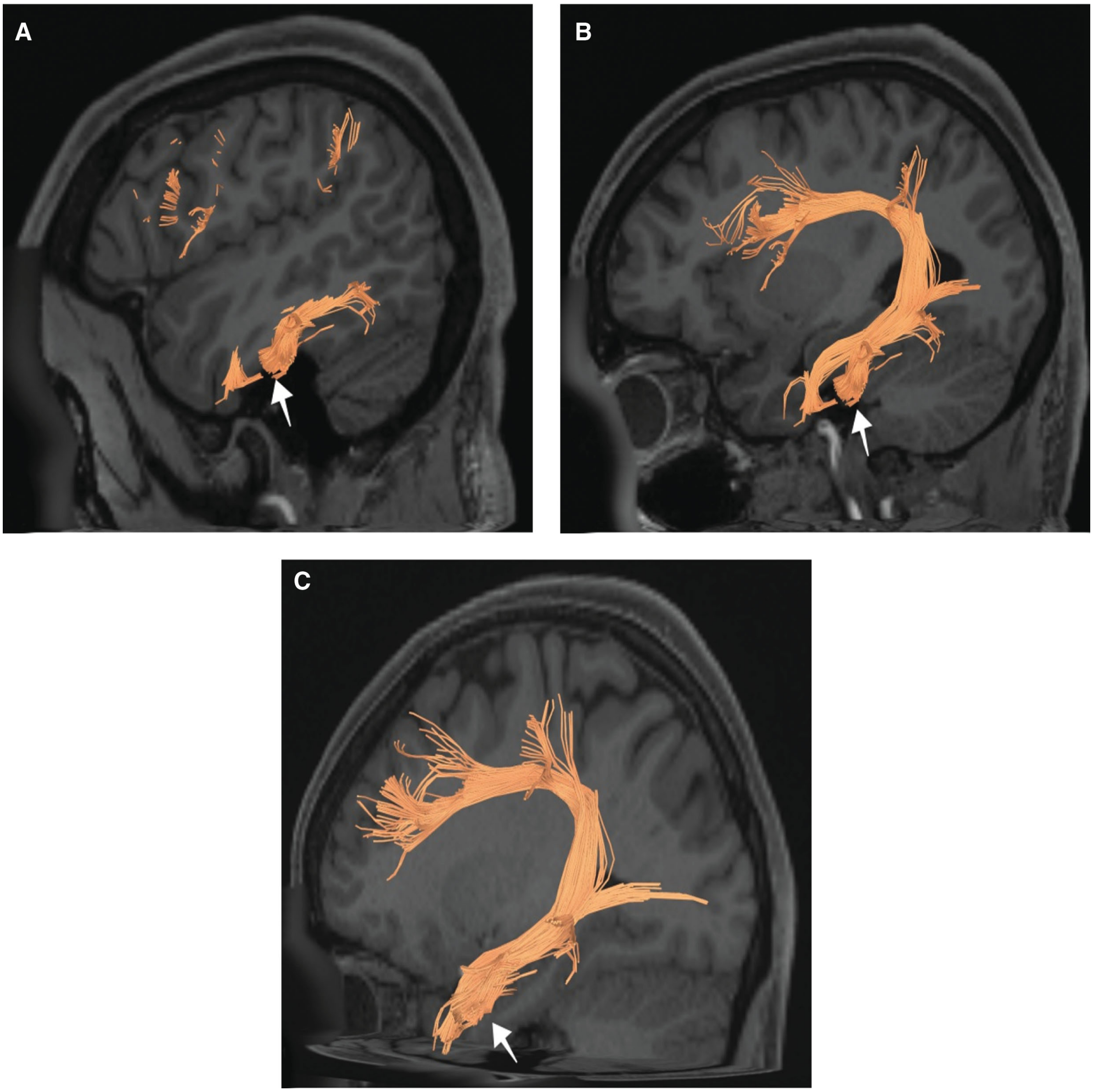

FIGURE 24. *Structural connectivity of TE2a in the left hemisphere, shown on T1-weighted MR images.* **A-C**, *Three sagittal views from* **A**, *most lateral to* **B** *and* **C**, *most medial showing projections to the frontal and occipital lobe and inferior parietal lobule. Light orange: white matter tracts of TE2a demonstrating connections with arcuate/SLF and ILF.*

IP0, PFop, 7PC, 7PL, and 7AL in the parietal lobe, and areas PH, FFC, FST, TPOJ2, and TPOJ3 in the occipital lobe (Figure 25).

What are its white matter connections? Area TE2p is structurally connected to the arcuate/SLF and local parcellations. White matter tracts of this parcellation are variable across individuals. Arcuate/SLF tracts wrap around the Sylvian fissure projecting toward the frontal lobe. The termination of the arcuate/SLF is unable to be delineated, as the tracts cannot be traced to specific parcellations. Local short association fibers connect to FFC, PH, TE2p, FFC, TE1m, TF, and TE2a (Figure 26). White matter tracts in the right hemisphere of TE2p have consistent occipital connections.

What is known about its function? The function of area TE2p appears primarily related to visual pathways.[1] Relative to TE2a,

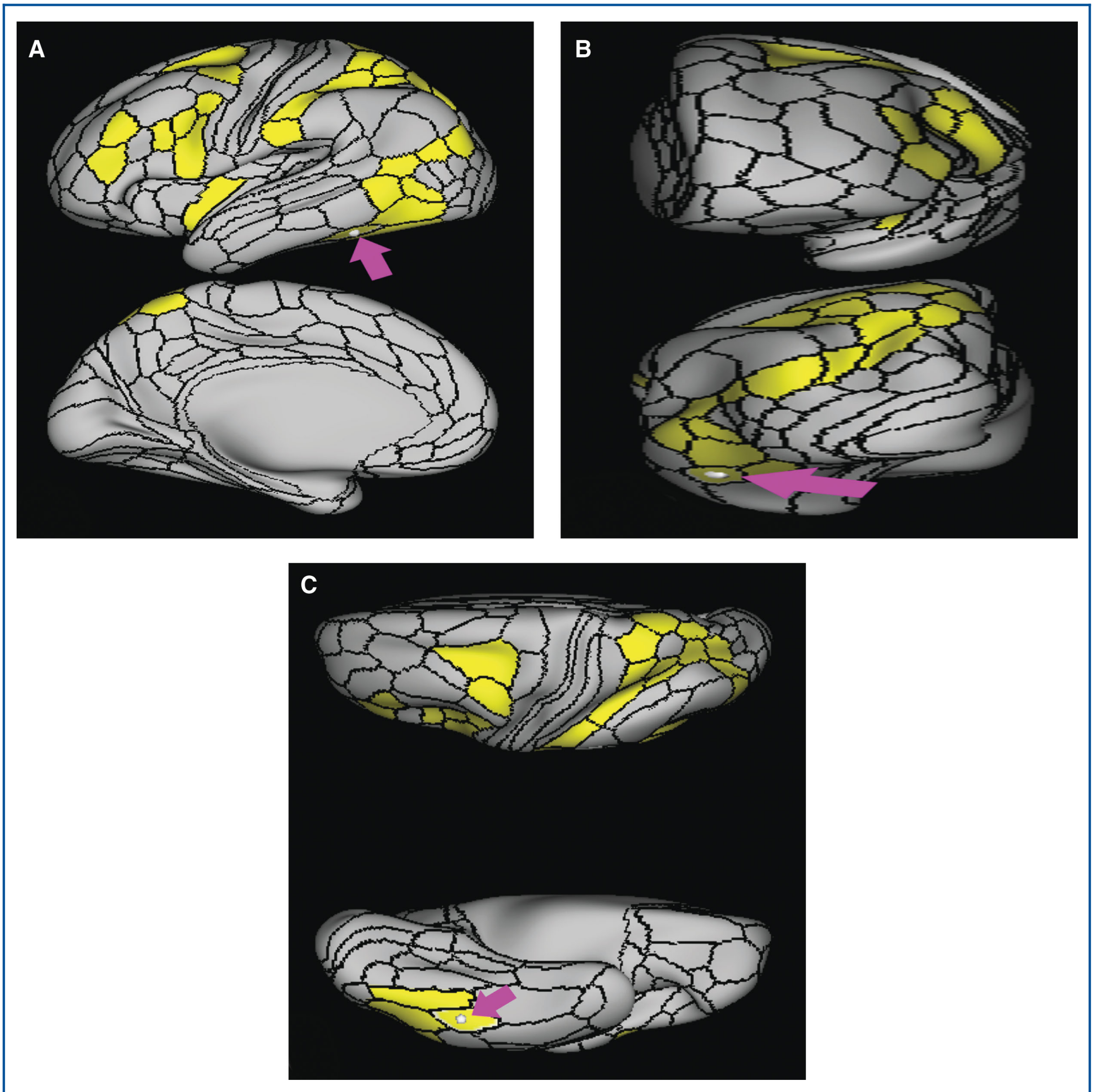

FIGURE 25. *Functional connectivity of TE2p demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation of interest.*

TE2p is more active in theory of mind tasks and motor tasks.[1] Notably, compared to the other TE1 and TE2 regions which are deactivated in the TOOL-AVG contrast, TE2p is activated unilaterally on the left in TOOL-AVG, demonstrating a possible role in object recognition.[1]

Area TF

Where is it? Area TF is found on the anterior part of the fusiform gyrus and the occipitotemporal sulcus. It occupies part of the lateral bank of the collateral sulcus.

What are its borders? Area TF borders TGv anteriorly, TE2a and TE2p laterally, PeEC medially, and FFC, ventral visual complex (VVC), parahippocampal area 2 (PHA2), and PHA3 posteriorly.

What is its functional connectivity? Area TF demonstrates functional connectivity to PeEC and TE2p (Figure 27).

What are its white matter connections? Area TF is structurally connected to the arcuate/SLF and ILF. The arcuate/SLF tracts wrap around the Sylvian fissure projecting toward the frontal lobe

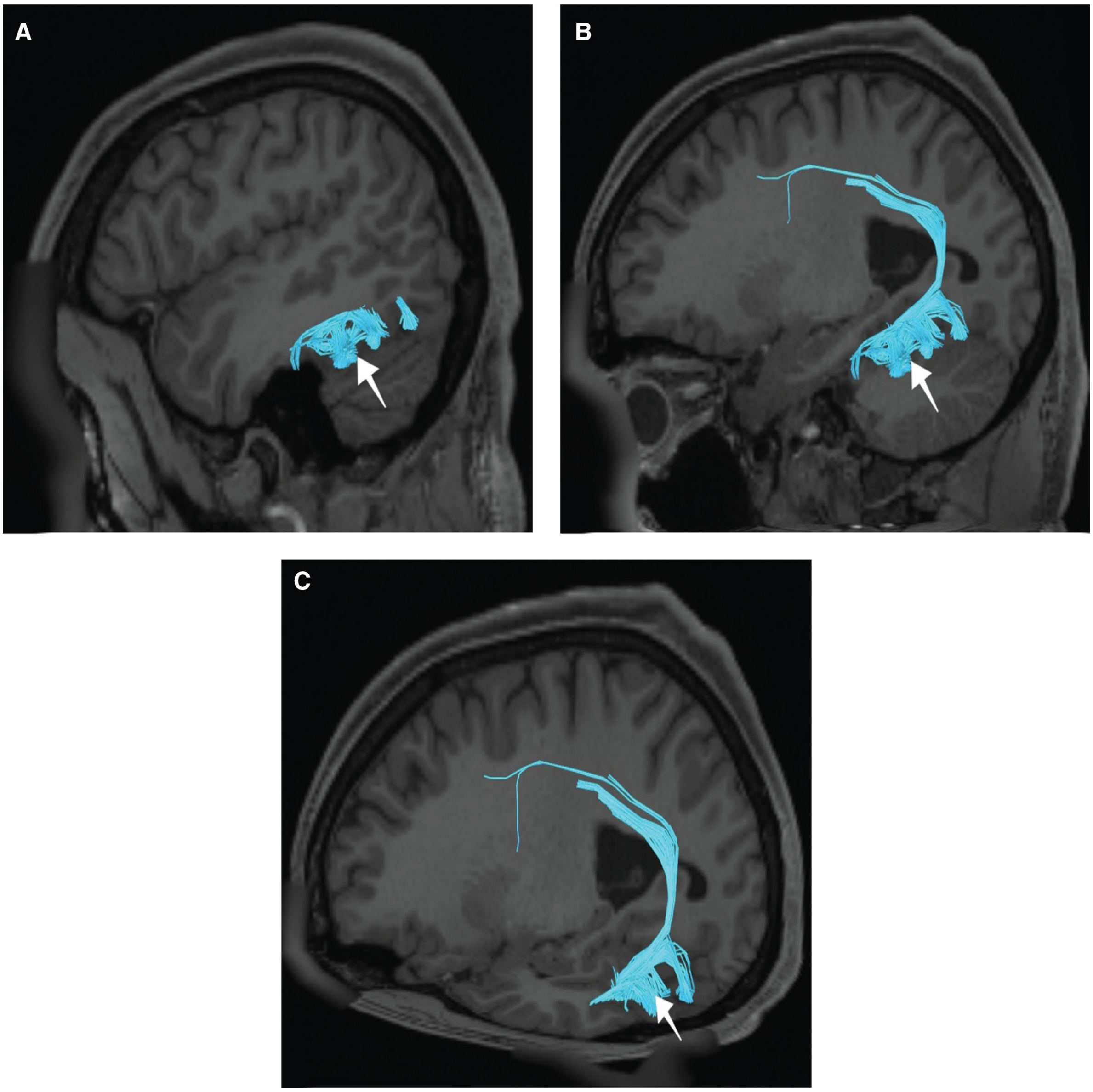

FIGURE 26. *Structural connectivity of TE2p in the left hemisphere, shown on T1-weighted MR images.* **A** *to* **C***, Three sagittal views from* **A***, most lateral to* **B** *and* **C***, most medial showing projections to frontal lobe. Light blue: white matter tracts of TE2p demonstrating connections with the arcuate/SLF.*

and turn medially to terminate at IFSa and 46. ILF terminations course through the inferior temporal lobe to terminate at V2, V3, V4, V3A, and V3b. Local short association bundles connect to PeEc, VVC, TE2p, and Te2a (Figure 28).

What is known about its function? Single neuron primate studies suggest that area TF may be involved in the maintenance of working memory in conjunction with inferior temporal and prefrontal regions.[3] Primate studies also show that removal of the posterior parahippocampal region (containing areas TF and TH) produces consistent deficits in spatial tasks involving object–place association.[6] In humans, TF is located in the anterior fusiform gyrus that is a hominid-specific structure.[7] The fusiform gyrus is important for visual perception such as in facial recognition, object recognition, and reading.[7]

The TE2 areas and TF comprise the ITG. Relative to TE2a that borders it laterally and superiorly, area TF is more activated in motor tasks, language recognition tasks, and theory of mind tasks.[1] Relative to TE2p posteriorly, area TF demonstrates greater activity in language recognition tasks and facial recognition tasks.[1]

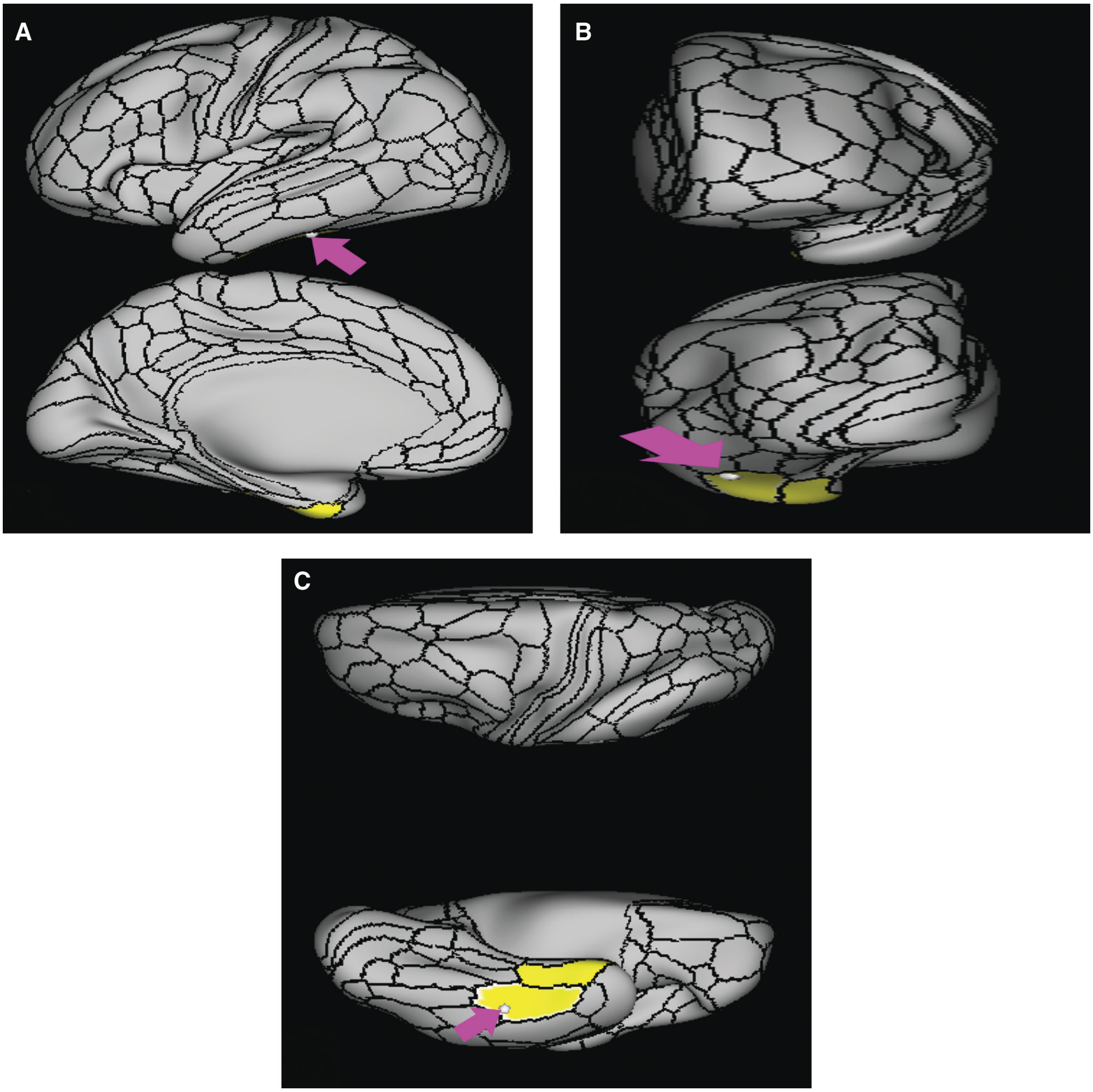

FIGURE 27. *Functional connectivity of TF demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation of interest.*

TG Areas

The anatomic locations of the parcellations that comprise the TG or temporal polar area are shown in Figure 29. The parcellations include TGd and TGv. The combined tractography of these parcellations is shown in Figure 30.

Area TGd

Where is it? Area TGd (TG dorsal) is found on the superior part of the temporopolar region. It is roughly anterior to the STG and MTG and wraps over the superior surface of the temporal planum polare just anterior to the limen insula.

What are its borders? Area TGd borders STGa, STSda, and TE1a posteriorly, TE2a and TGv inferiorly, Pir and PI on its anteromedial edge, and PeEC on its posterior mesial border.

What is its functional connectivity? Area TGd demonstrates functional connectivity to 8AV, 8BL, 9a, 9p, 9m, 44, 45, 47s,

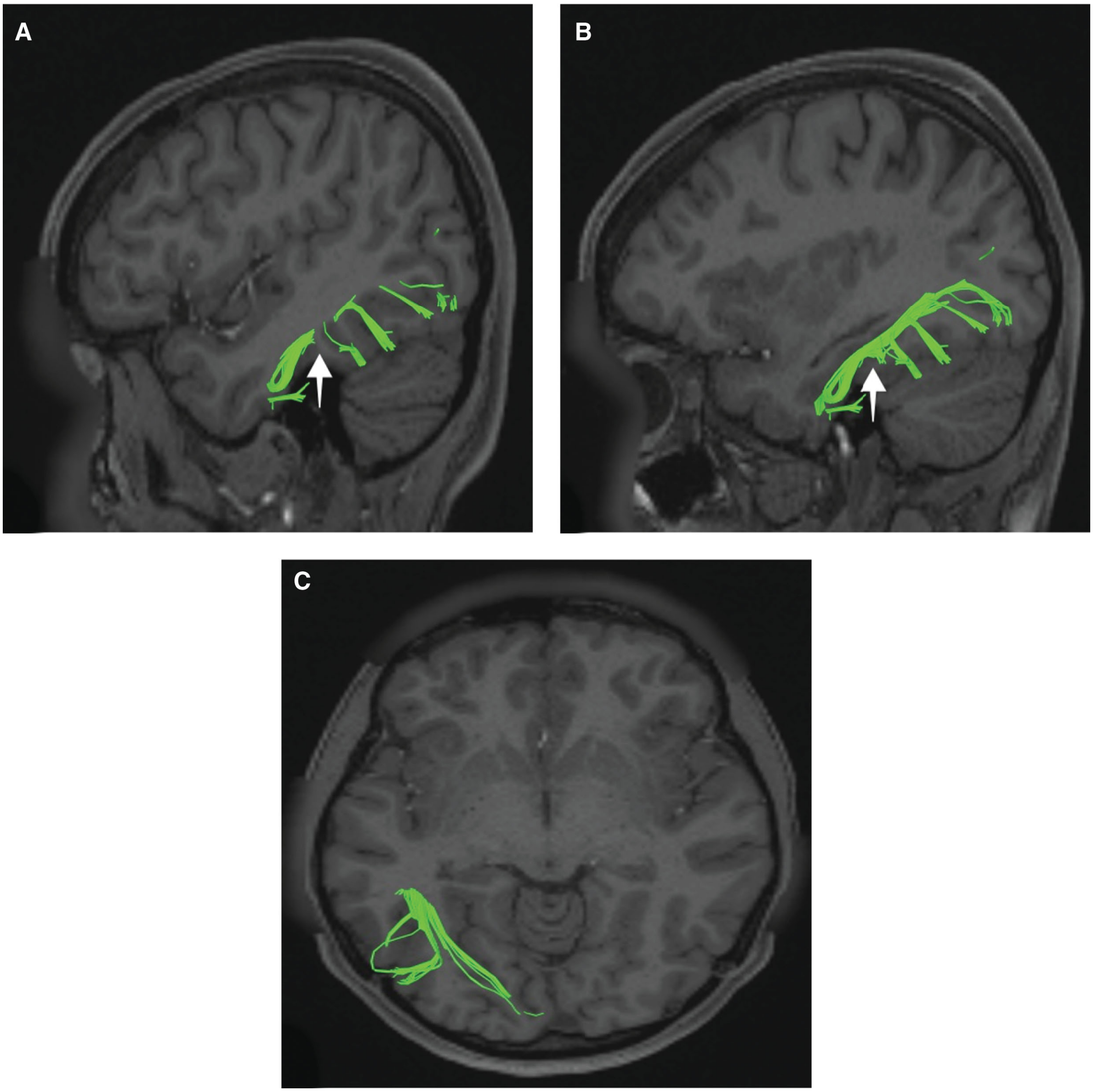

FIGURE 28. *Structural connectivity of TF in the left hemisphere, shown on T1-weighted MR images. Sagittal views of* **A**, *lateral and* **B**, *medial planes, and* **C**, *axial views showing projections to the occipital lobe. Light green: white matter tracts of TF demonstrating connections with the ILF.*

47L, 10v, 10r, and SFL in the frontal lobe, areas STSva, STSvp, STSda, STSdp, TGv, STGa, PeEc, the hippocampus, and TE1a in the temporal lobe, and areas PGs, PGi, 7m, d23ab, 31pv, and 31pd in the parietal lobe (Figure 31).

What are its white matter connections? Area TGd is structurally connected to the uncinate fasciculus and ILF. Many individuals also have connections through the extreme/external capsule toward the parieto-occipital sulcus and occipital lobe. The uncinate fasciculus wraps medially around the fibers travelling toward the occipital lobe, these fibers course through the extreme/external capsule through the posterior temporal lobe to terminate at DVT, V1, V3, V2, V6, and 7PL. The uncinate fasciculus projects to the frontal lobe through the insula to terminate at FOP4, FOP5, 44, and 45. ILF fibers course through the inferior temporal lobe to terminate at V1 and V2 (Figure 32).

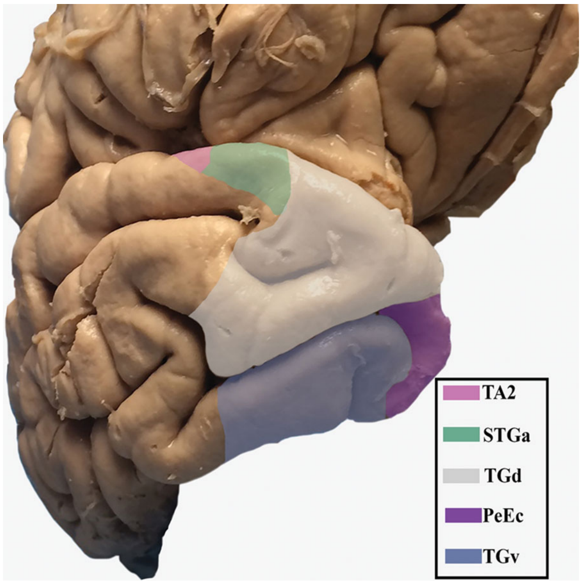

FIGURE 29. *Anatomic view of the TG parcellations shown on the right anterior temporal pole of a cadaver brain.*

What is known about its function? Areas TGd and TGv make up the temporal polar cortex, a paralimbic region important for social and emotional processing, auditory and visual aspects of facial recognition, emotional processing of auditory, olfactory and visual stimuli, and theory of mind.[8] TGd, like TGv, is activated in the language-related task contrasts suggesting a role in ventral stream language processing along with its neighbors STGa, STSda, STSva, and TE1a.[1] Compared to TGv inferiorly, TGd is deactivated vs activated in motor tasks in response to a visual cue and relational primary contrasts (ie, distinguishing objects based on feature dimensions).[1]

Area TGvWhere is it?

Area TGv (TG ventral) is found on the inferior temporal polar region just anterior to the ITG and fusifom gyrus.

What are its borders? Area TGv borders TE2a posteriorly on its lateral surface, TF posteriorly on its basal surface, and TGd superiorly. PeEc makes up its medial basal surface.

What is its functional connectivity? Area TGv demonstrates functional connectivity to areas 45 and TGd (Figure 33).

What are its white matter connections? Area TGv is structurally connected to the ILF. ILF projections travel through the inferior temporal lobe to terminate at V1, V2, V3, and V4 (Figure 34).

What is known about its function? Areas TGv and TGd make up the temporal polar cortex described in the previous section. Area TGv, like TGd, is activated in language-related task contrasts suggesting a role in ventral stream language processing.[1] Compared to TGd superiorly, TGv is activated vs deactivated in motor tasks in response to a visual cue and relational primary contrasts (ie, distinguishing objects based on feature dimensions).[1]

Medial Temporal Areas

The anatomic locations of the parcellations that comprise the medial temporal area are shown in Figure 35. The parcellations include PreS, EC, PeEc, parahippocampal area 1 (PHA1), PHA2, and PHA3. The combined tractography of these parcellations is shown in Figure 36.

Area PreS

Where is it? Area PreS is found on the posterior superior surface of the parahippocampal gyrus.

What are its borders? Area PreS borders the hippocampus medially, and the entrorhinal cortex anteriorly. Its posterior border is made up of RSC (retrosplenial cortex) and the ProS (prostriate region; which are discussed in other sections). PHA1 is its inferior border.

What is its functional connectivity? Area PreS demonstrates functional connectivity areas 8AD and i6-8 in the frontal lobe, areas PHA1, PHA2, and the hippocampus in the temporal lobe, areas RSC, Pros, d23ab, v23ab, 31a, 31pv, 7m, 7pm, POS1, POS2, IP1, and PGs in the parietal lobe, and area V1 in the occipital lobe (Figure 37).

What are its white matter connections? Area PreS is structurally connected to the cingulum, precuneus and occipital lobe. Cingulum projections run superior to the corpus callosum to end at anterior cingulate cortex and frontal lobe parcellations a24, 9m, 10d, and p32. There are PreS fibers that project posteriorly to end at occipital and precuneus areas V1, V2, V6, POS1, POS2, and 7m. Local short association fibers are connected to EC and PeEc (Figure 38).

What is known about its function? The presubiculum lies medial to the subiculum—a region of the hippocampus that primate studies suggest is involved in the processing of spatial information.[9] Area PreS contains more myelin than the hippocampal cortex, and relative to PHA1 inferiorly, contains more myelin, is thinner, and demonstrates less activity during tasks related to working memory, language processing, and theory of mind.[1] Relative to PHA1, PreS shows greater activity during motor tasks.[1]

Area EC

Where is it? Area EC is found on the medial posterior surface of the uncus.

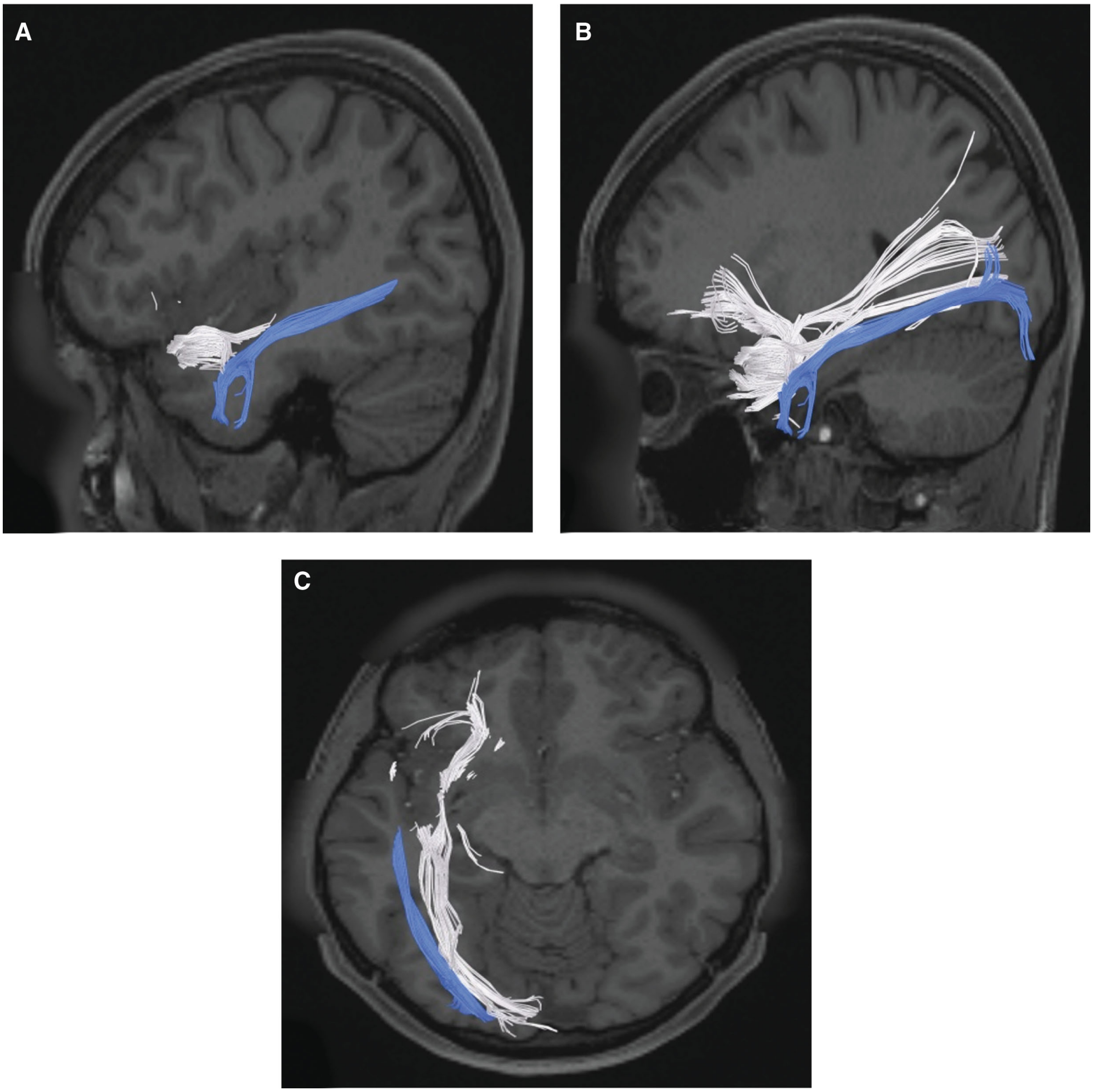

FIGURE 30. *Combined structural connectivity of the TG parcellations, shown on T1-weighted MR images. Sagittal views of* **A***, lateral and* **B***, medial planes.* **C***, Axial view. Tracks correspond to TGd (white) and TGv (blue).*

What are its borders? Area EC borders the presubiculum posteriorly, as well as PHA1. Its inferior and anterior neighbor is PeEC.

What is its functional connectivity? Area EC demonstrates functional connectivity to area 8ad in the frontal lobe, areas TE1a, PeEc, and the hippocampus in the temporal lobe, and area PGs in the parietal lobe (Figure 39).

What are its white matter connections? Area EC is structurally connected to the cingulum. Cingulum fibers span the entire cingulate cortex to terminate anteriorly at a24pr and p24. There are posterior projections from the cingulum that travel toward the parieto-occipital sulcus to terminate at DVT and POS2 (Figure 40).

What is known about its function? The EC is thought to be involved in both the rapid encoding of new associations and

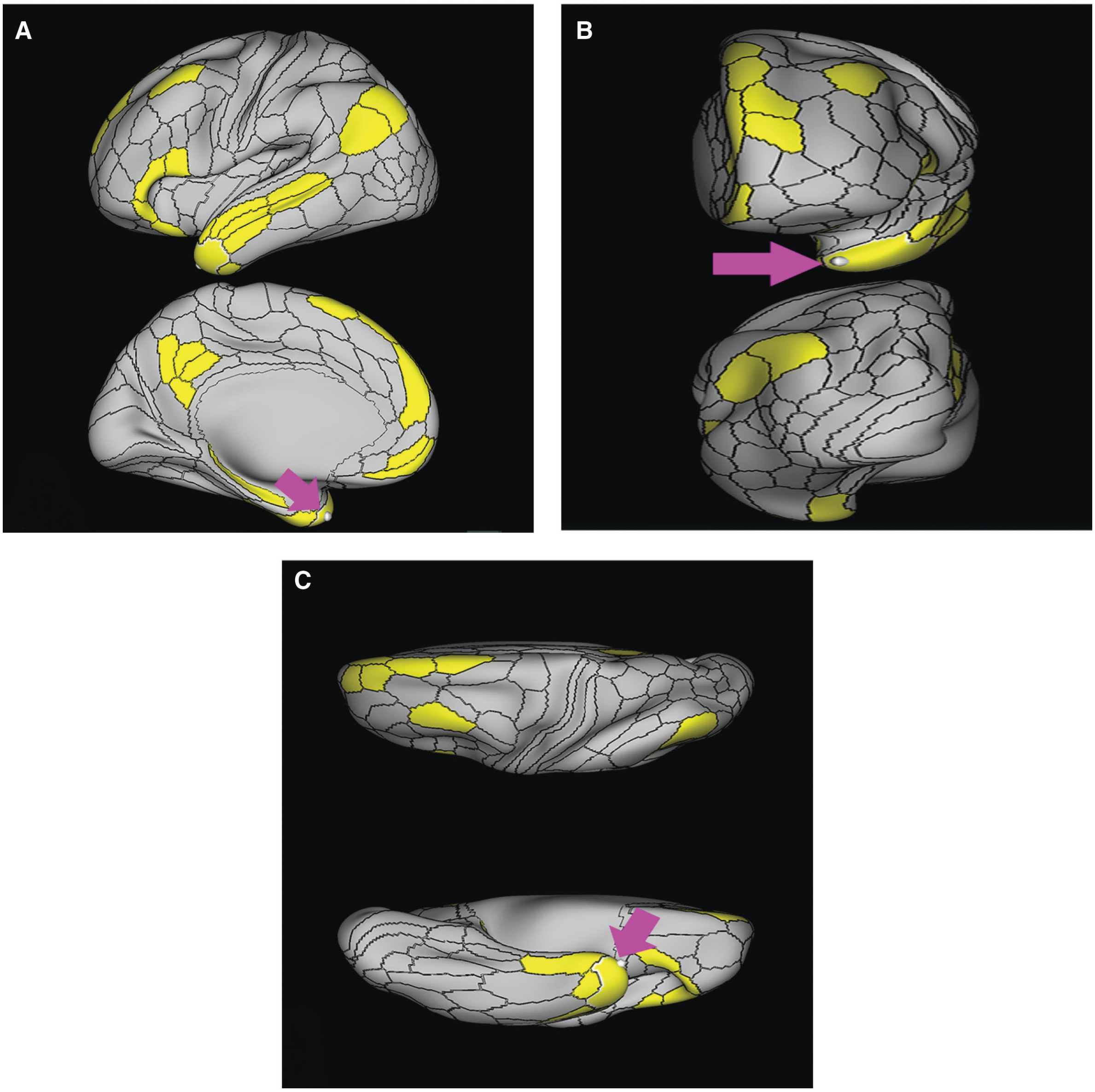

FIGURE 31. *Functional connectivity of TGd demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation of interest.*

in the consolidation of memory in connection with the medial prefrontal cortex.[10] Relative to the PeEC that borders the region inferiorly and medially, the EC contains more myelin, is thinner, and has different functional connectivity.[1] It is less activated in primary task contrasts, ie completed tasks vs baseline fixation, and activated rather than deactivated in working memory of body images.[1] Relative to area PHA1 posteriorly, the EC contains more myelin, is thinner, and is less activated during language tasks and theory of mind tasks.[1]

Area PeEC

Where is it? Area PeEC is found on the anterior portions and inferior surface of the uncus extending to the collateral sulcus.

What are its borders? Area PeEC borders areas TGv and TGd anteriorly and TF laterally. Its posterior borders are PHA2 and PHA3.

FIGURE 32. *Structural connectivity of TGd in the left hemisphere, shown on T1-weighted MR images. Sagittal views of* **A**, *lateral and* **B**, *medial planes and* **C**, *axial views showing projections to the frontal and occipital lobes. White: white matter tracts of TGd demonstrating connections with the uncinate fasciculus and ILF.*

What is its functional connectivity? Area PeEC demonstrates functional connectivity to area IFSa the frontal lobe, areas EC, TF, PHA2, and PHA3 in the temporal lobe, area IP0 in the parietal lobe, and area PH in the occipital lobe (Figure 41).

What are its white matter connections? Area PeEC is structurally connected to the ILF. ILF projections travel through the inferior temporal lobe to end at PH, TPOJ3, and MT. In some individuals there are fibers that parallel the ILF to terminate at the medial occipital lobe at V1 (Figure 42).

What is known about its function? The perirhinal cortex contributes to declarative memories transmitted between cortical areas and the hippocampus.[11] The perirhinal cortex region adds semantic knowledge to aid in item identification.[11] In addition, the perirhinal cortex integrates item information with

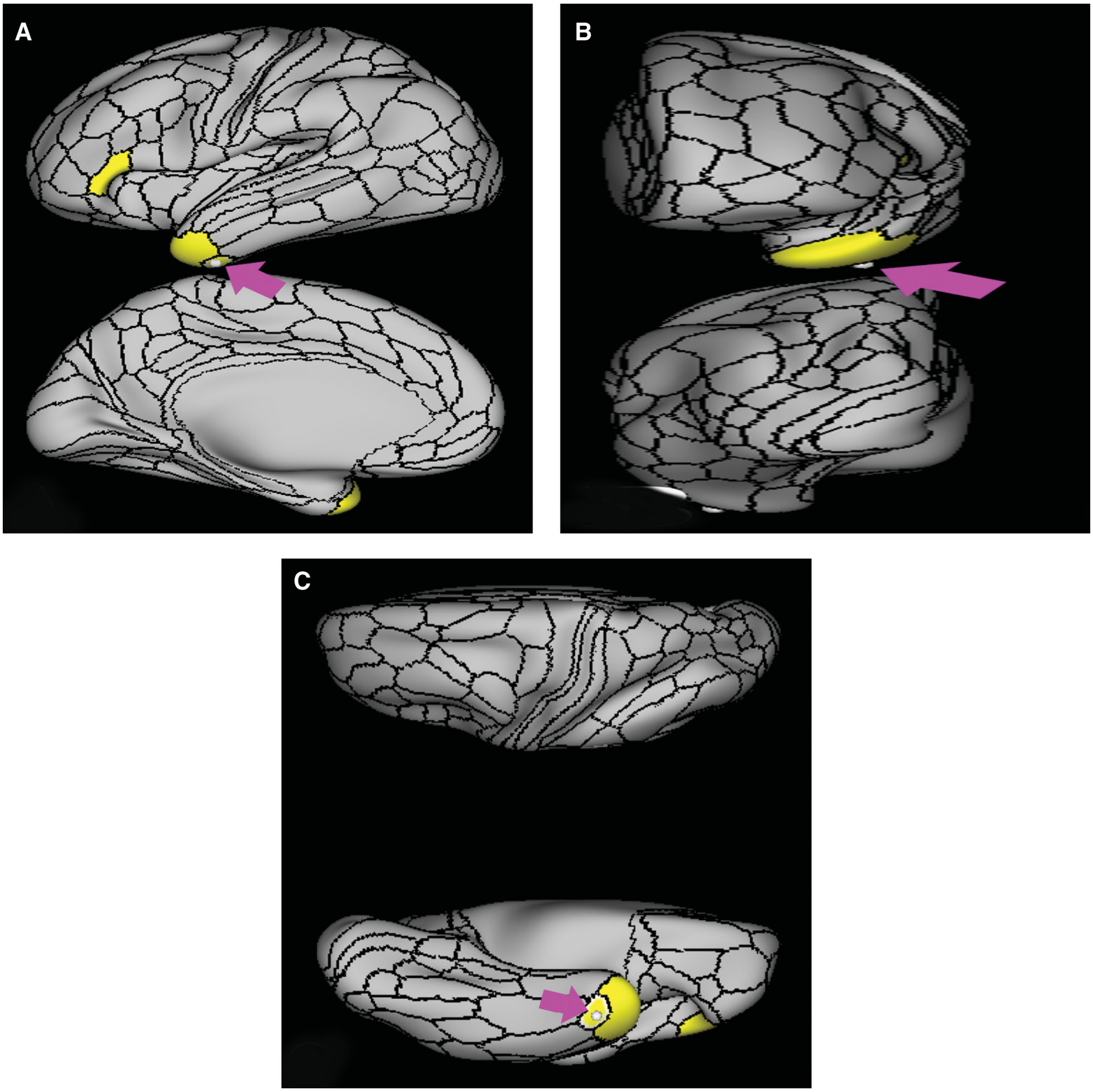

FIGURE 33. *Functional connectivity of TGv demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation of interest.*

spatio-temporal information and transmits this data to the hippocampus via the EC.[11] The HCP authors were unable to reliably separate the perirhinal cortex and ectorhinal cortex, and therefore combined them as a single region.[1] Area PeEC can be distinguished from neighboring regions based on increased activation in working memory primary task contrasts and increased activation in selective recognition of faces. Due to its particular affinity for facial recognition tasks compared to its neighbors, the HCP authors hypothesize that the region may be the site of the anterior temporal face patch.[1,12,13]

Area PHA1

Where is it? Area PHA1 is a long thin area on the medial portion of the parahippocampal gyrus.

What are its borders? Area PHA1 borders area PreS superiorly and PHA2 inferiorly. Its posterior border is VMV1 and its anterior border is EC.

What is its functional connectivity? Area PHA1 demonstrates functional connectivity to areas 10r and 8ad in the frontal lobe,

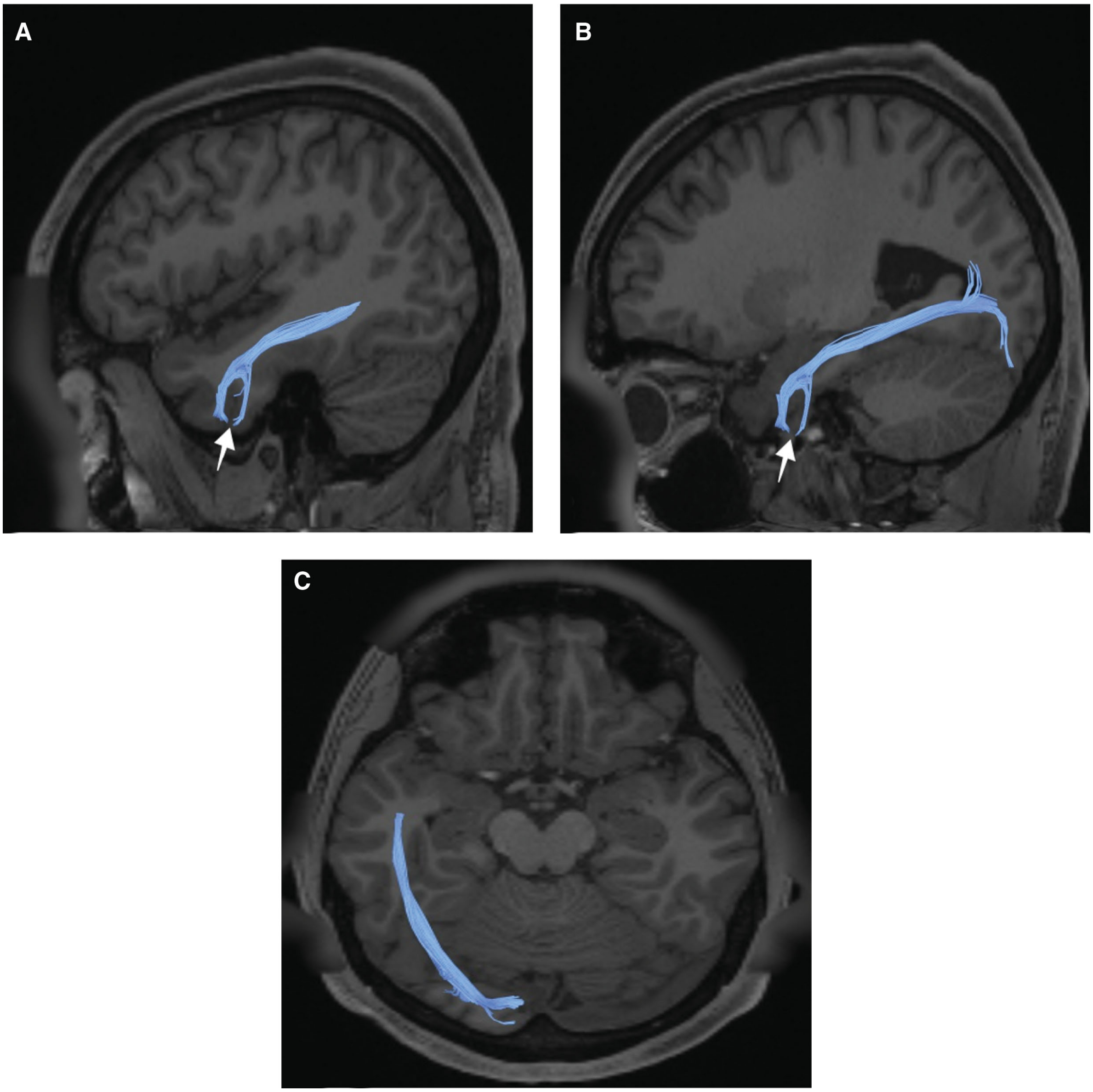

FIGURE 34. *Structural connectivity of TGv in the left hemisphere, shown on T1-weighted MR images.* **A** *and* **B**, *Sagittal and* **C**, *axial views showing projections to the occipital lobe. Light blue: white matter tracts of TGv demonstrating connections with the ILF.*

areas PHA2, PHA3, VMV1, PreS, the hippocampus in the temporal lobe, and areas ProS, POS1, PGp, and PGs in the parietal lobe (Figure 43).

What are its white matter connections? Area PHA1 is connected to local parcellations. Local anterior fibers connect to PeEC. Local posterior fibers connect to PH. The exact terminations of the local connections are inconsistent across individuals (Figure 44).

What is known about its function? The parahippocampal cortex is involved in visuospatial processing and episodic memory by processing contextual information.[14] The anterior parahippocampal cortex is involved in encoding information without regard for stimulus category (scenes vs objects) or modality (word vs picture) and interfaces with the hippocampus, retrosplenial, and perirhinal memory systems, while the posterior parahippocampal cortex is involved with pictorial scene analysis, namely processing spatial features of visual scenes.[15]

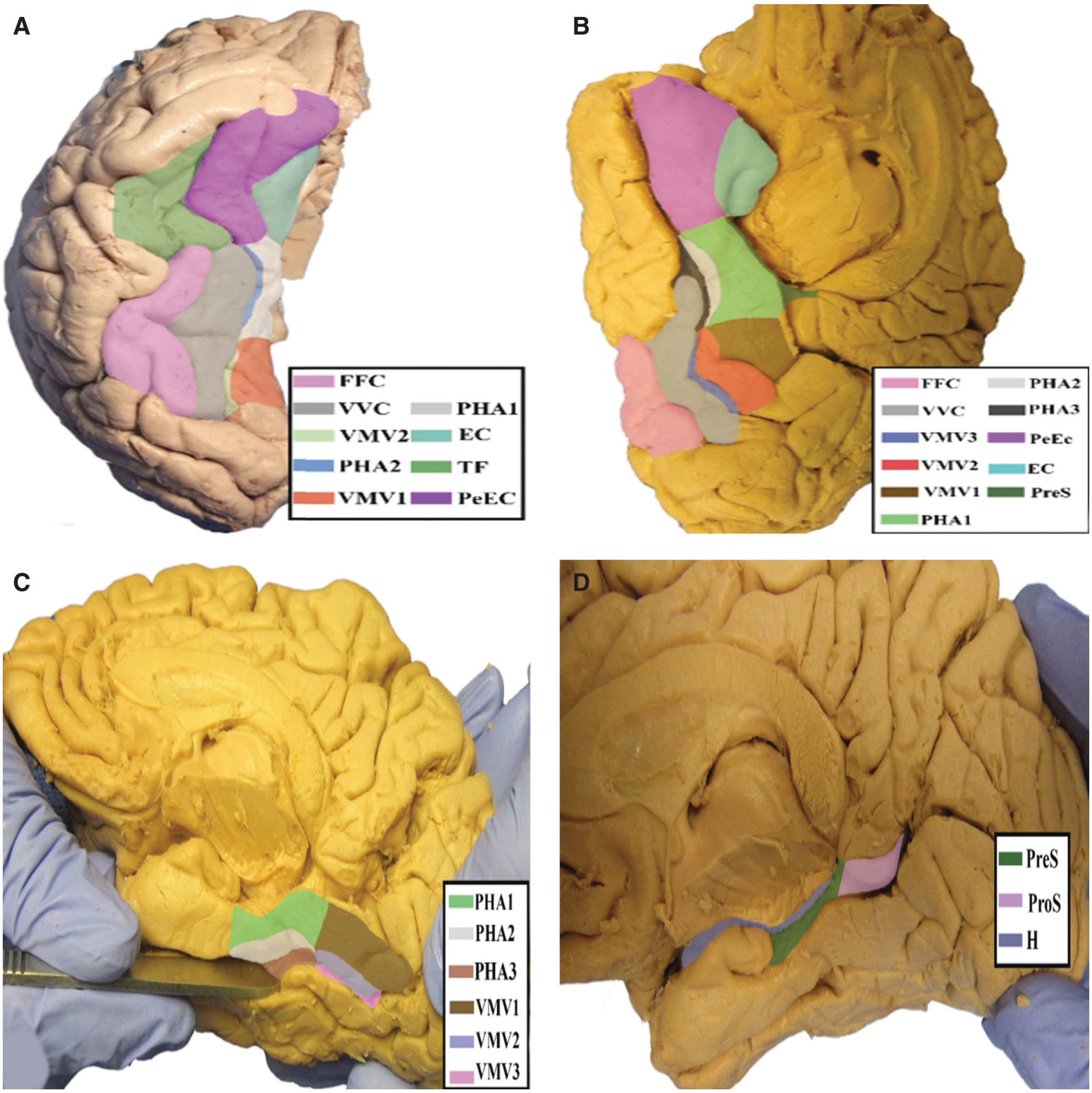

FIGURE 35. *Anatomic view of the medial temporal parcellations shown on the right hemisphere of a cadaver brain.* **A**, *Inferior view of the temporal lobe.* **B**, *Inferomedial view demonstrating the parahippocampal gyrus parcellations of the temporal lobe.* **C**, *Inferomedial view of the temporal lobe with widening of the collateral sulcus to show the extent of PHA3 and VMV3.* **D**, *Medial view of the temporal lobe with widening of retrosplenial space to show extension of PreS.*

Like both PHA2 and PHA3, PHA1 is activated in the PLACE-AVG contrast and deactivated in the FACE-AVG contrast, suggesting a role in place/scene recognition rather than face recognition.[1] However, PHA1 is less deactivated in face recognition than PHA2 and PHA3 inferiorly.[1]

Area PHA2

Where is it? Area PHA2 is found on parahippocampal gyrus, primarily on its inferior surface, just adjacent to the collateral sulcus.

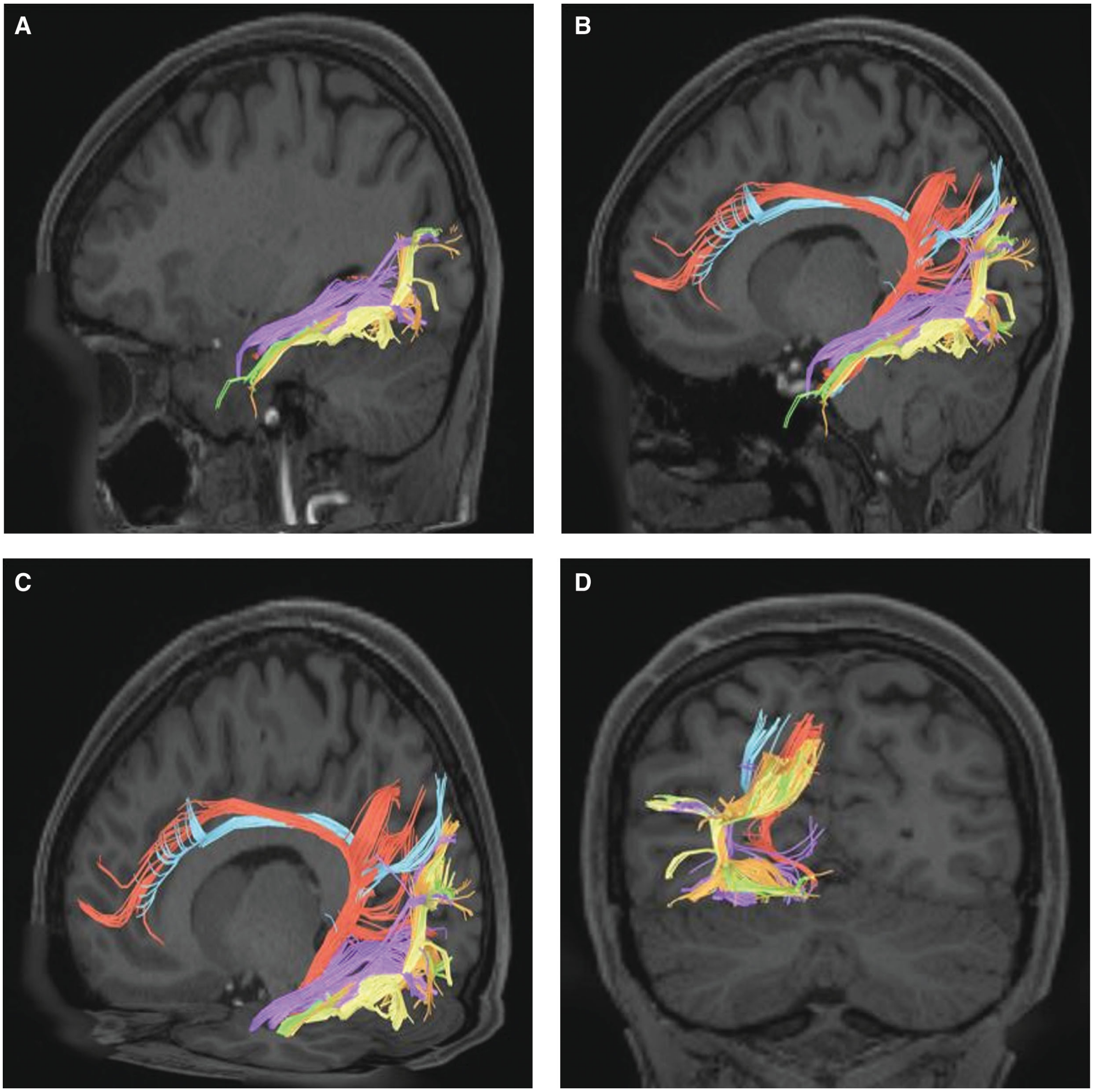

FIGURE 36. *Combined structural connectivity of the medial temporal parcellations, shown on T1-weighted MR images.* **A** *to* **C**, *Three sagittal views from* **A**, *most lateral to* **B**, *and* **C**, *most medial.* **D**, *Coronal view. Tracks correspond to PreS (red), EC (light blue), PeEc (purple), PHA1 (light green), PHA2 (yellow), and PHA3 (orange).*

What are its borders? Area PHA2 is a long thin anterior posterior area between PHA1 superiorly and PHA3 inferiorly. It has a small posterior border with VMV2.

What is its functional connectivity? Area PHA2 demonstrates functional connectivity to areas 8AD, 47m, and i6-8 in the frontal lobe, areas PHA1, PHA3, PreS, and the hippocampus in the temporal lobe, areas ProS, 7pm, PCV, DVT, POS1, IP0, PGp, and PGs in the parietal lobe, and area TPOJ3 in the occipital lobe (Figure 45).

What are its white matter connections? Area PHA2 is structurally connected to the ILF. There are anterior projections from the ILF that terminate at PeEc. The posterior terminations of the

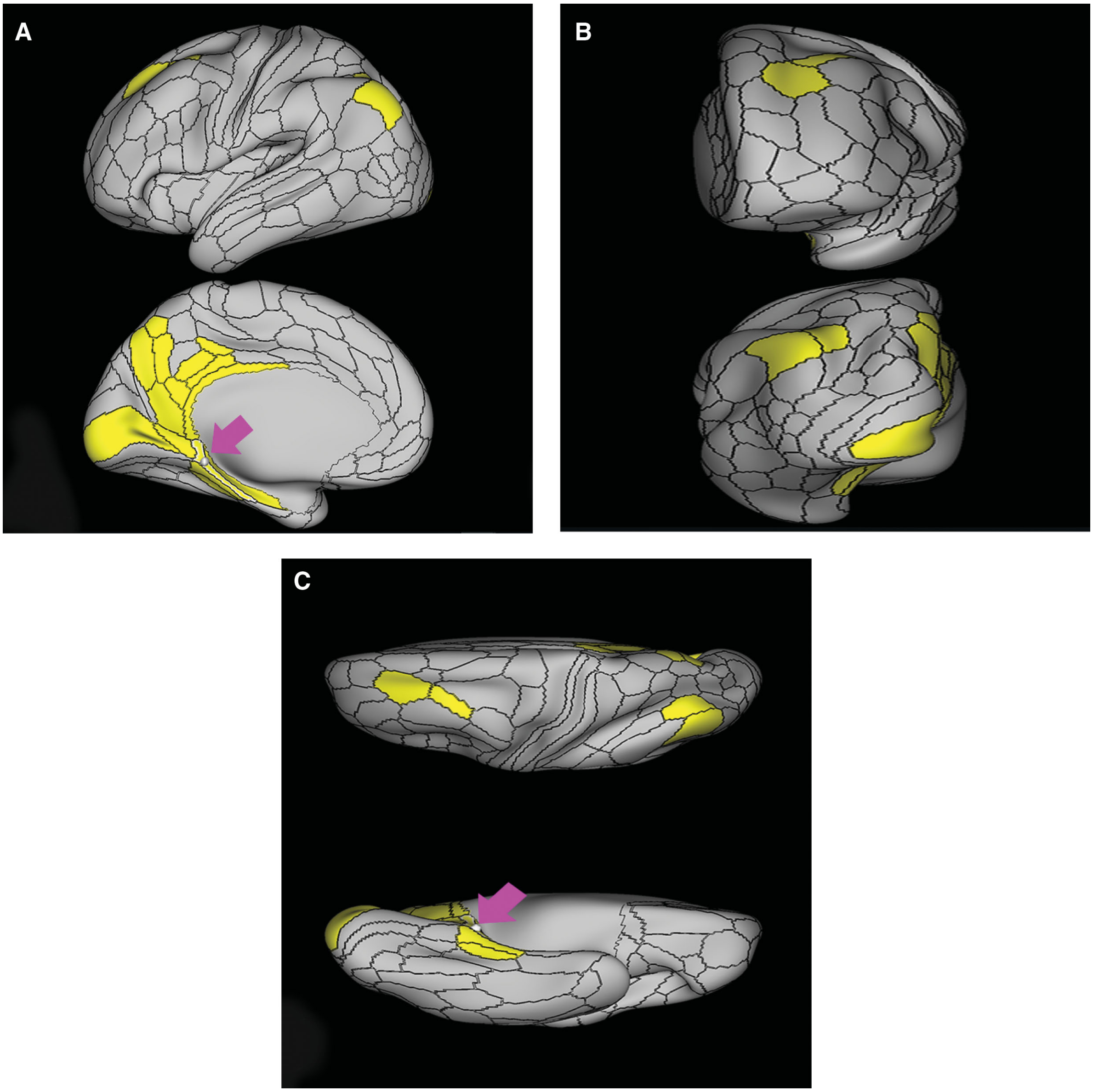

FIGURE 37. *Functional connectivity of PreS demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation of interest.*

ILF terminate at V1, V2, and V3. The exact terminations of the local connections are inconsistent across individuals (Figure 46).

What is known about its function? The parahippocampal cortex is involved in visuospatial processing and episodic memory by processing contextual information.[14] The anterior parahippocampal cortex is involved in encoding information without regard for stimulus category (scenes vs objects) or modality (word vs picture) and interfaces with the hippocampus, retrosplenial, and perirhinal memory systems, while the posterior parahippocampal cortex is involved with pictorial scene analysis, namely processing spatial features of visual scenes.[15]

Like both PHA1 and PHA3, PHA2 is activated in the PLACE-AVG contrast and deactivated in the FACE-AVG contrast, suggesting a role in place/scene recognition rather than face recog-

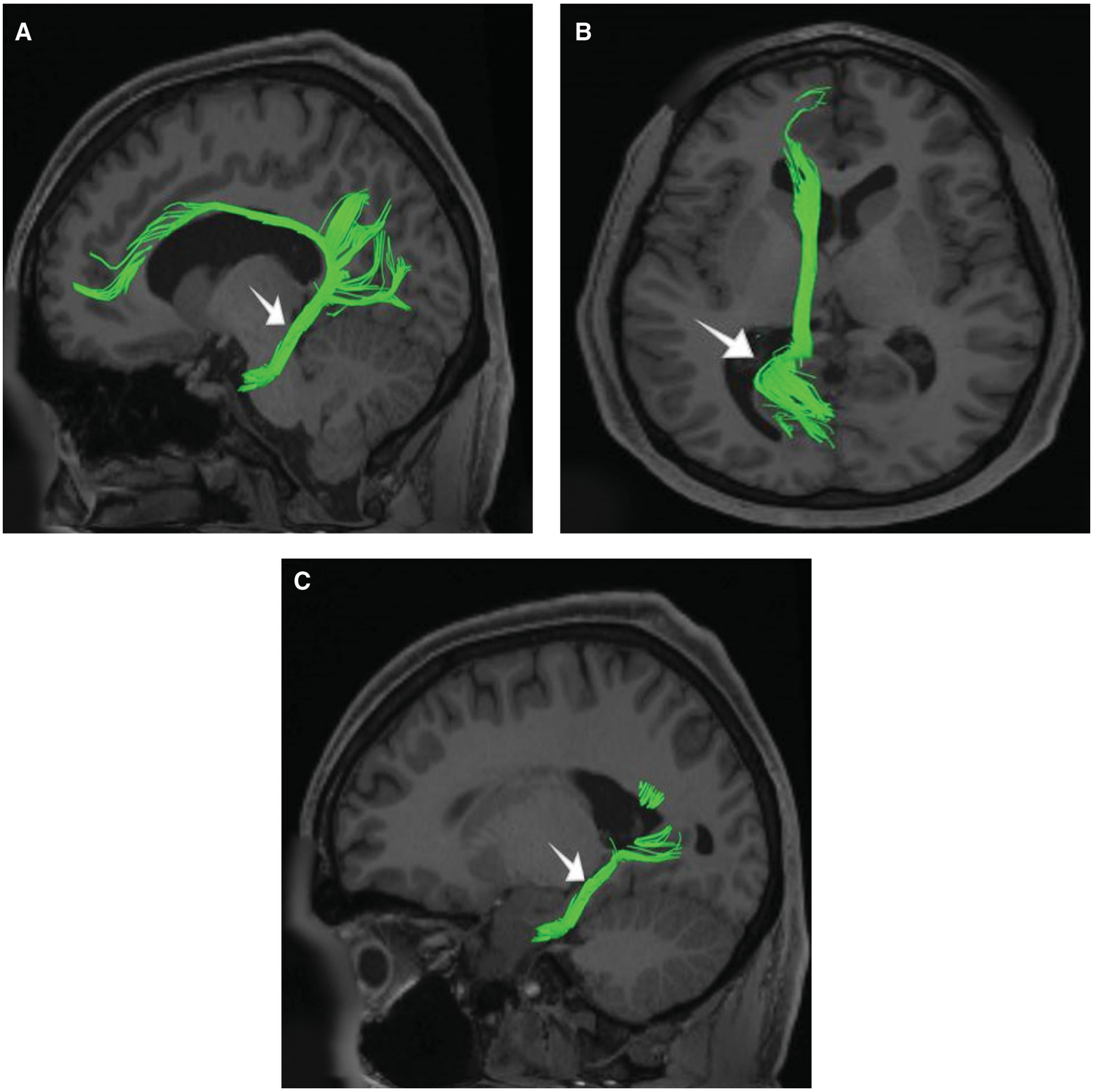

FIGURE 38. *Structural connectivity of PreS in the left hemisphere, shown on T1-weighted MR images. Sagittal views of* **A**, *medial and* **B**, *lateral planes, and* **C**, *coronal views showing projections to the cingulum, occipital lobe, and the contralateral hemisphere. Dark green: white matter tracts of PreS demonstrating connections with the cingulate fibers.*

nition.[1] Area PHA2 is more deactivated than PHA1 in facial recognition tasks.[1]

Area PHA3

Where is it? Area PHA3 is located in the parahippocampal gyrus, primarily inside the collateral sulcus.

What are its borders? Area PHA3 borders PHA2 superiorly, and VVC and TF inferiorly. Its posterior border is with VMV2 and VMV3, and its anterior border is PeEC.

What is its functional connectivity? Area PHA3 demonstrates functional connectivity to areas 6a and IFSa in the frontal lobe, areas PHT, PHA1, PHA2, VMV2, and PeEc in the temporal lobe,

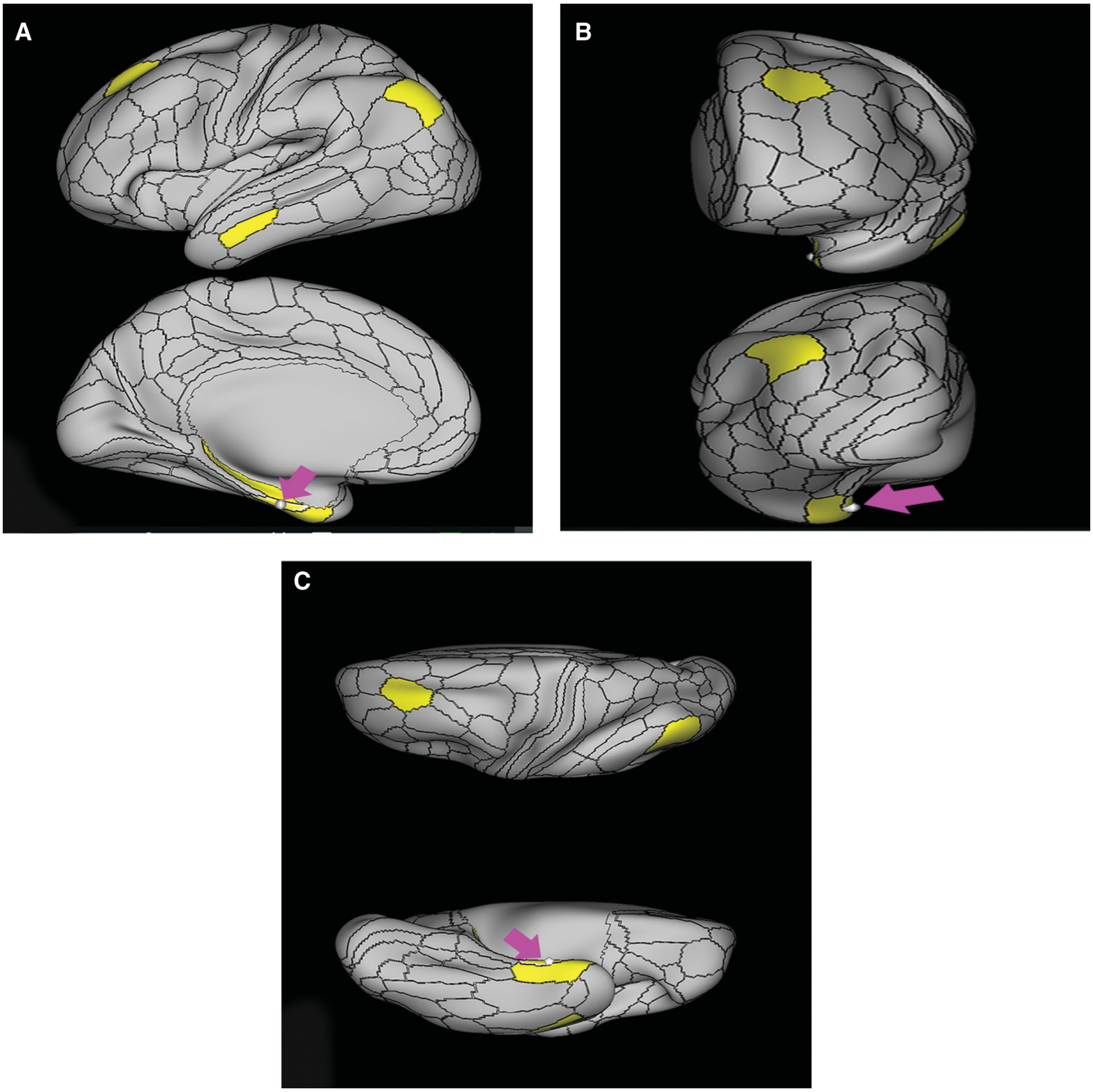

FIGURE 39. *Functional connectivity of EC demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation of interest.*

areas 23c, 7pl, 7am, 7pm, PCV, DVT POS1, MIP, LIPd, AIP, PGp, and PFt in the parietal lobe, and areas TPOJ3 and VVC in the occipital lobe (Figure 47).

What are its white matter connections? Area PHA3 is structurally connected to the ILF. There are anterior projections from the ILF that terminate at TGd. The posterior terminations of the ILF terminate at VVC and FFC. There are fibers that run parallel to the ILF and terminate at the occipital lobe at V1, V2, and V6. The exact terminations of the local connections are inconsistent across individuals (Figure 48).

What is known about its function? The parahippocampal cortex is involved in visuospatial processing and episodic memory by processing contextual information.[14] The anterior parahippocampal cortex is involved in encoding information

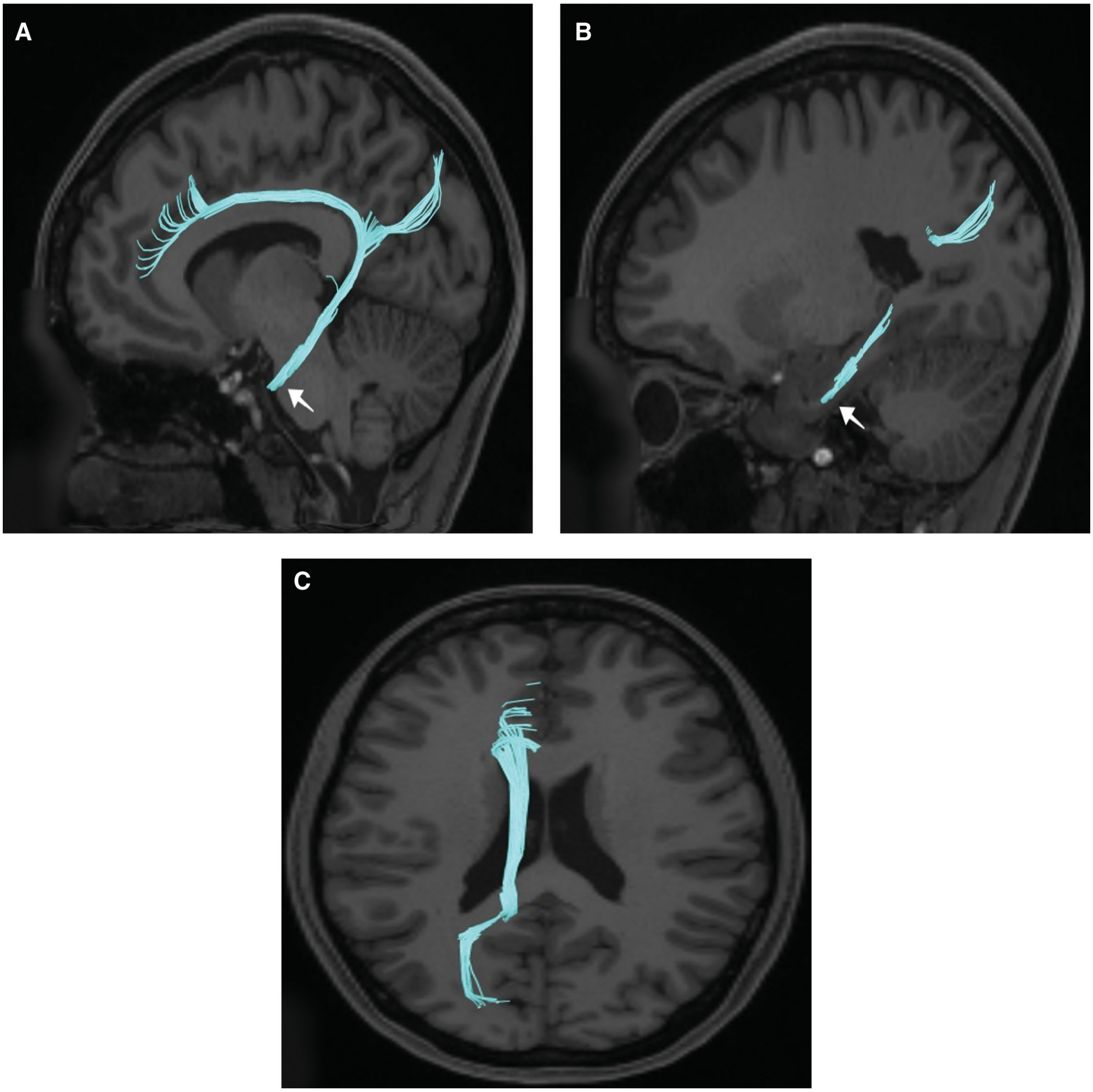

FIGURE 40. *Structural connectivity of EC in the left hemisphere, shown on T1-weighted MR images. Sagittal views of* **A**, *medial and* **B**, *lateral planes and* **C**, *axial views showing projections to the cingulum and parieto-occipital sulcus. Light blue: white matter tracts of EC demonstrating connections with the cingulate fibers.*

without regard for stimulus category (scenes vs objects) or modality (word vs picture) and interfaces with the hippocampus, retrosplenial, and perirhinal memory systems, while the posterior parahippocampal cortex is involved with pictorial scene analysis, namely processing spatial features of visual scenes.[15] Relative to PHA2, area PHA3 demonstrates greater activity in tool-related recognition tasks.[1]

DISCUSSION

The temporal lobe is a well-known area to the neurosurgical community as we have been removing it for decades.[16,17] Much of the debate about temporal lobe epilepsy surgery has revolved around the balance between epilepsy freedom versus the risk of cognitive impairments.[17] Regardless of the merits of either

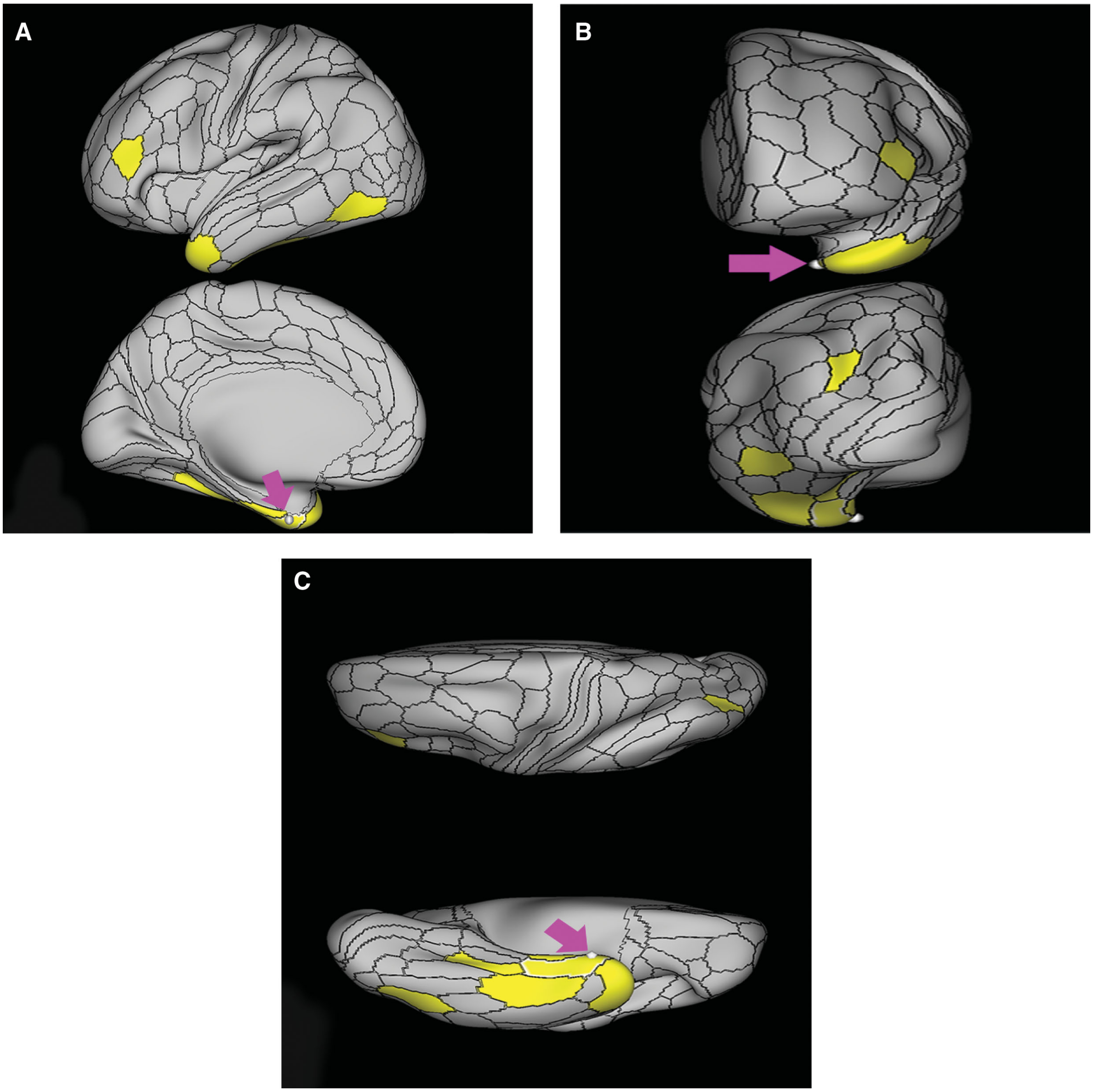

FIGURE 41. *Functional connectivity of PeEC demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation of interest.*

argument, it is likely that the best possible outcome is obtained by merely disconnecting the offending circuits with as little collateral damage as possible. Given the precision and simplicity of treatments such as laser interstitial thermal therapy, the greatest barrier to this technology becoming the reality for temporal lobe epilepsy treatment are our limits in precisely knowing the epileptic focus, and as a corollary, our limited understanding of the connections and functional segregation of the temporal lobe.

The Human Connectome Project data and our own analysis make it clear that the traditional methods of classifying temporal lobe regions, namely by calling temporal gyri T1, T2, and so on, has no basis in functional or organizational anatomy and should be replaced with one which better fits the data. Given that temporal lobe areas like TE1p straddle gyri and sulci and that there are four critically connected language-type areas in the STS, it is clear that while previous organizational schema of the

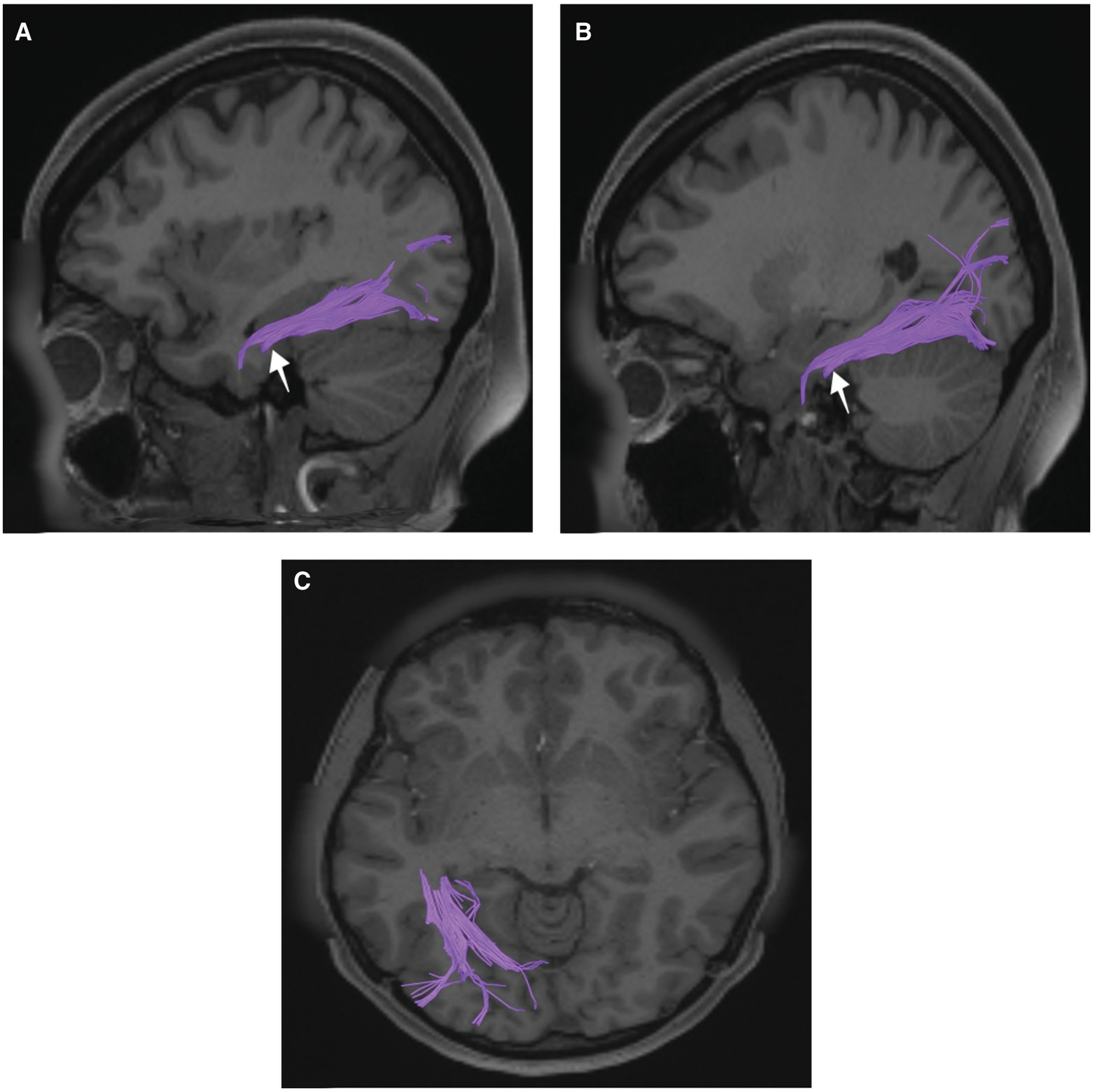

FIGURE 42. *Structural connectivity of PeEc in the left hemisphere, shown on T1-weighted MR images. Sagittal views of* **A**, *medial and* **B**, *lateral planes, and* **C**, *axial views showing projections to the occipital lobe. Purple: white matter tracts of PeEC demonstrating connections with ILF.*

brain have been convenient, they diverge significantly from true functional organization of the brain.

Like other areas of the brain, it is impossible to make a perfect classification system for parts of the temporal lobe as some areas connect to more than one fiber system (TGd being one obvious example as it connects to the SLF/arcuate, ILF, and uncinate), and several areas appear functionally multimodal. Thus, trying to reduce this to a simple organizational scheme is fraught with problems. However, it can be helpful in simplifying the general patterns of connectivity to something learnable. Therefore, we propose the following scheme:

Lateral: SLF/arcuate system areas that include all 4 STS areas, TE1a, TE1m, TE1p, PHT, TE2a, and that seem to be part of the semantic network and semantic processing.[1,2,5]

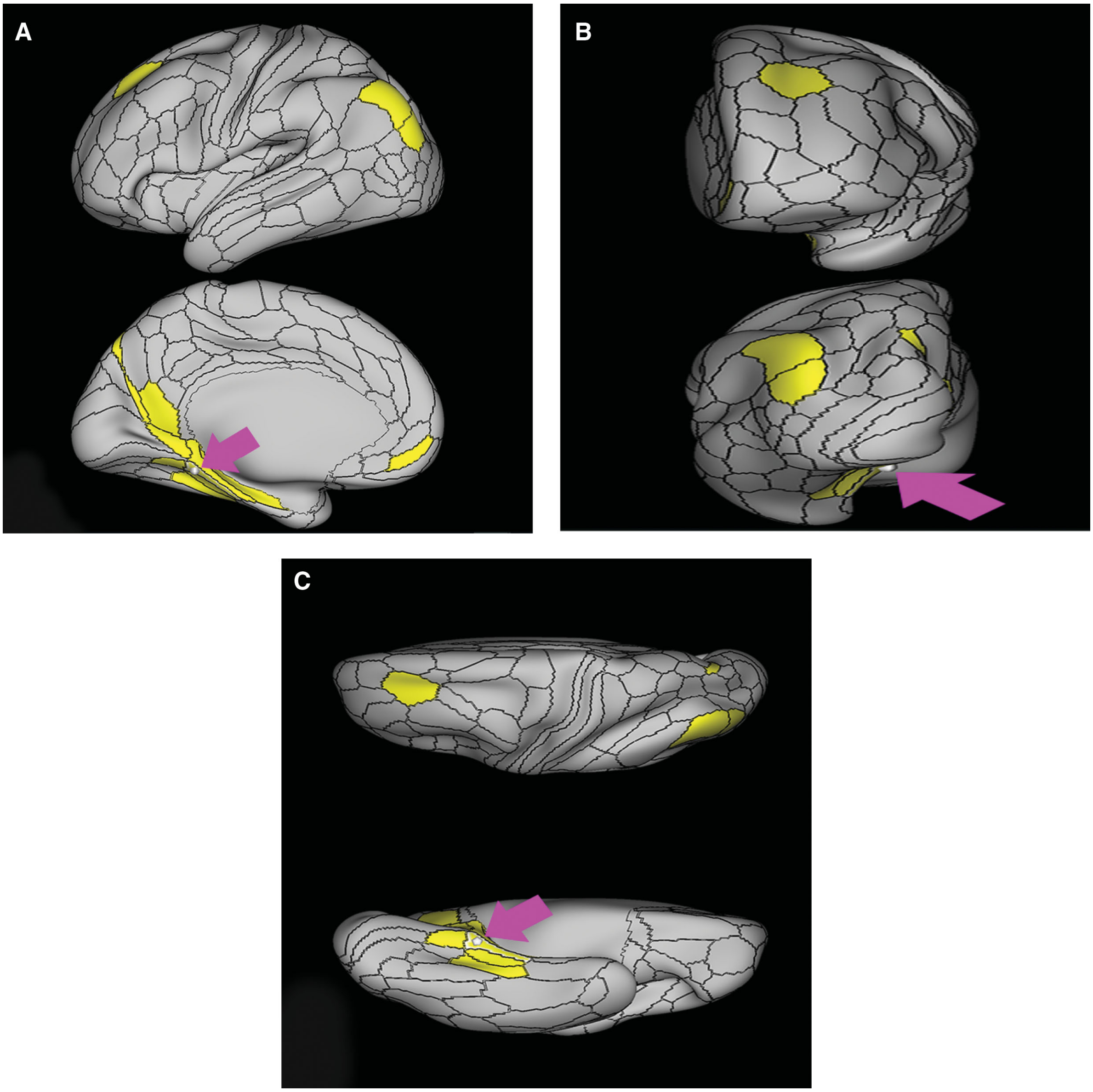

FIGURE 43. *Functional connectivity of PHA1 demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation of interest.*

Polar: Uncinate connected areas, namely TGd and TGv, which have mixed inputs and likely play a role in emotional processing as well as other functions.[8]

Inferior: ILF connected areas such as TE2a, TE2p, TF, and PeEC that likely play some role in visual processing.[1,7]

Medial: Areas involved in the hippocampus and cingulate system, such as EC, PreS, PHA1, PHA2, and PHA3, which are mostly interconnected, though project into the cingulum as well as having some connections to the visual system via the ILF.

What follows is a brief description of the connectional anatomy of these subunits and a few insights we have had while studying these regions.

The Lateral Temporal System

It is a very interesting aspect of temporal lobe anatomy that its medial structures do not connect to its lateral structures, as the major white matter anatomy in the temporal lobe largely runs anterior-to-posterior more than medial-to-lateral. It is possible to

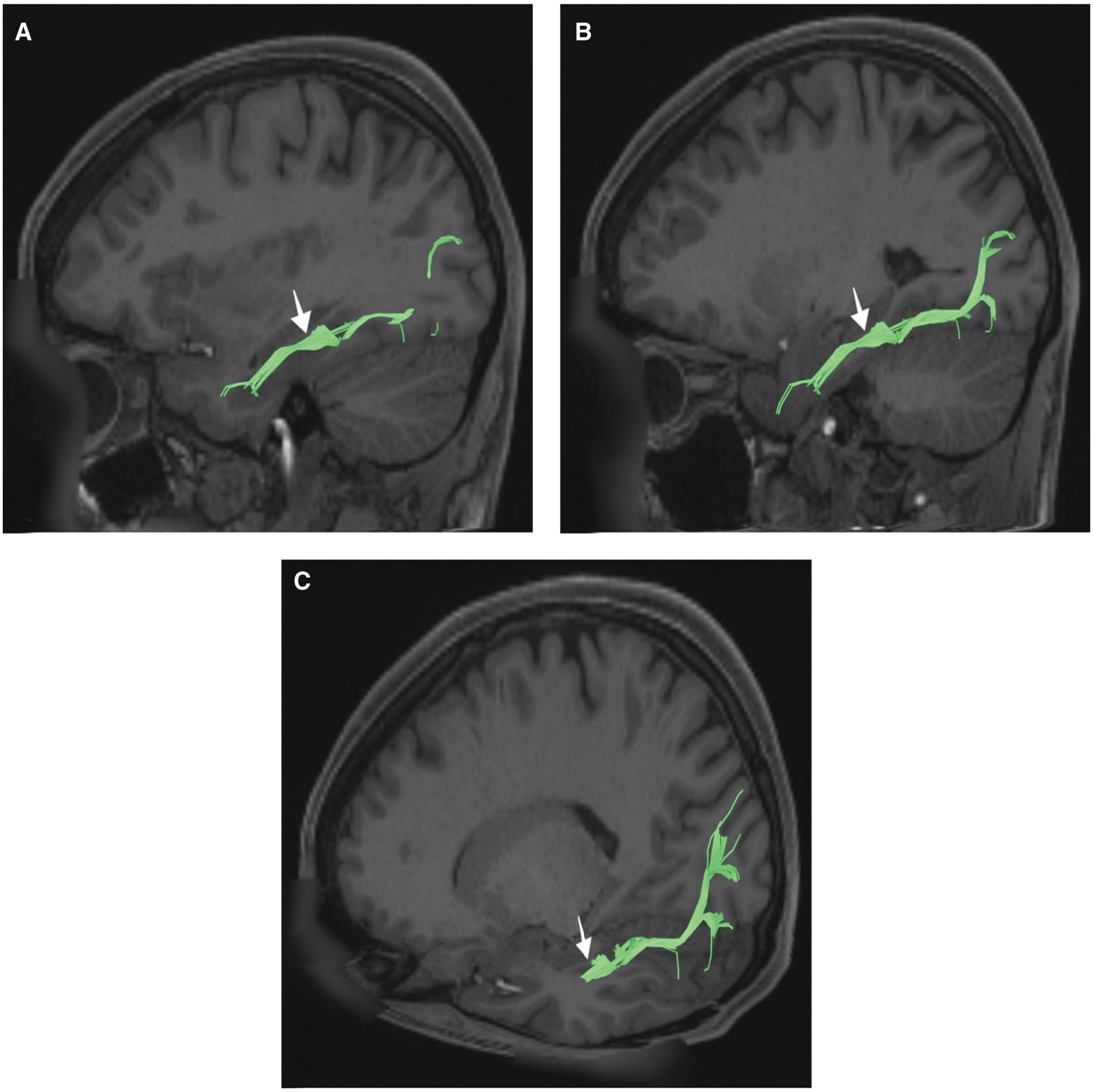

FIGURE 44. *Structural connectivity of PHA1 in the left hemisphere, shown on T1-weighted MR images.* **A-C***, Three sagittal views from* **A***, most lateral to* **B** *and* **C***, most medial showing projections to the inferior temporal lobe and the occipital lobe. Light green: white matter tracts of PHA1 demonstrating connections posteriorly and anteriorly with local parcellations.*

trace a plausible pathway from a lateral parcellation to a medial one (ie TE2a to TF to PeEC to EC), but there is no evidence of major connections between them. This is an observation we have long exploited to remove large gliomas adjacent to the hippocampus while preserving the lateral system.

It is not surprising to find that the posterior temporal lobe has dense connections to the posterior frontal and parietal lobes via the SLF/arcuate complex, as this has been known for decades. What is relatively surprising is that when studying the functional and structural connectivity maps, the temporal lobe parcellations appear to segregate into two distinct clusters:

Superior cluster: TE1a, STSda, STSdp, STSva, STSvp.

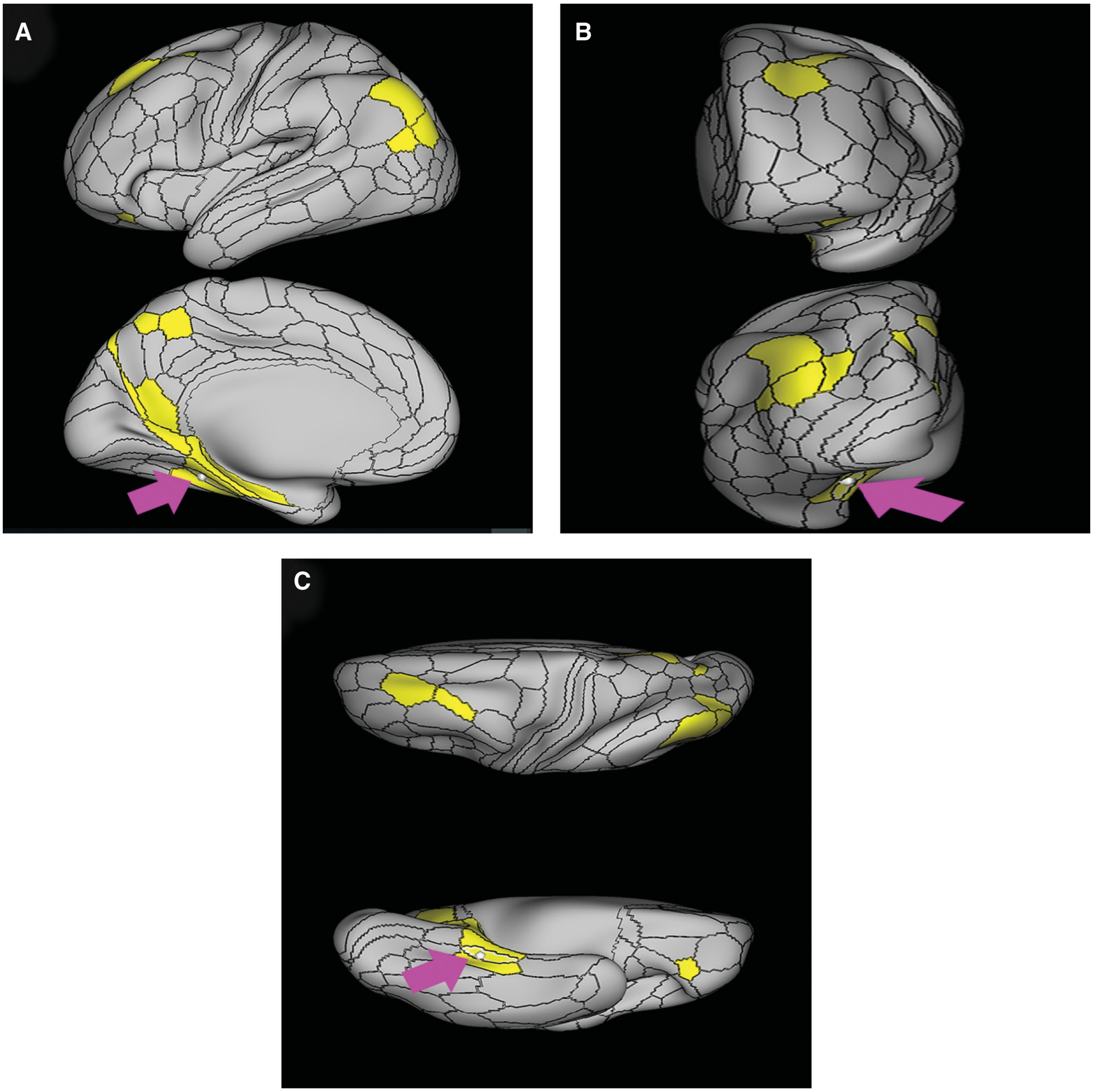

FIGURE 45. *Functional connectivity of PHA2 demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation of interest.*

Inferior cluster: TE1m, TE1p, TE2a, PHT.

Besides the general interconnections between each other, and the general pattern of functional connectivity (ie superior cluster areas seem more connected to each other than they do to their neighbors and vice versa), the most notable difference between these systems is their distal targets. Superior cluster fibers tend to end in the posterior inferior frontal gyrus, while inferior cluster fibers tend to end in more superior parts of the frontal lobe such as middle frontal gyrus or inferior frontal sulcus regions. This suggests they play different roles in the network. Regardless, it is one observation worth studying in more detail.

Which Areas are the Language Areas?

It is likely many or even all of these areas play some role in language production, so to ask a more relevant question: Which areas are the indispensable ones for language production? It is highly likely that this differs greatly between subjects, and we need better metrics for the essentiality of specific areas for

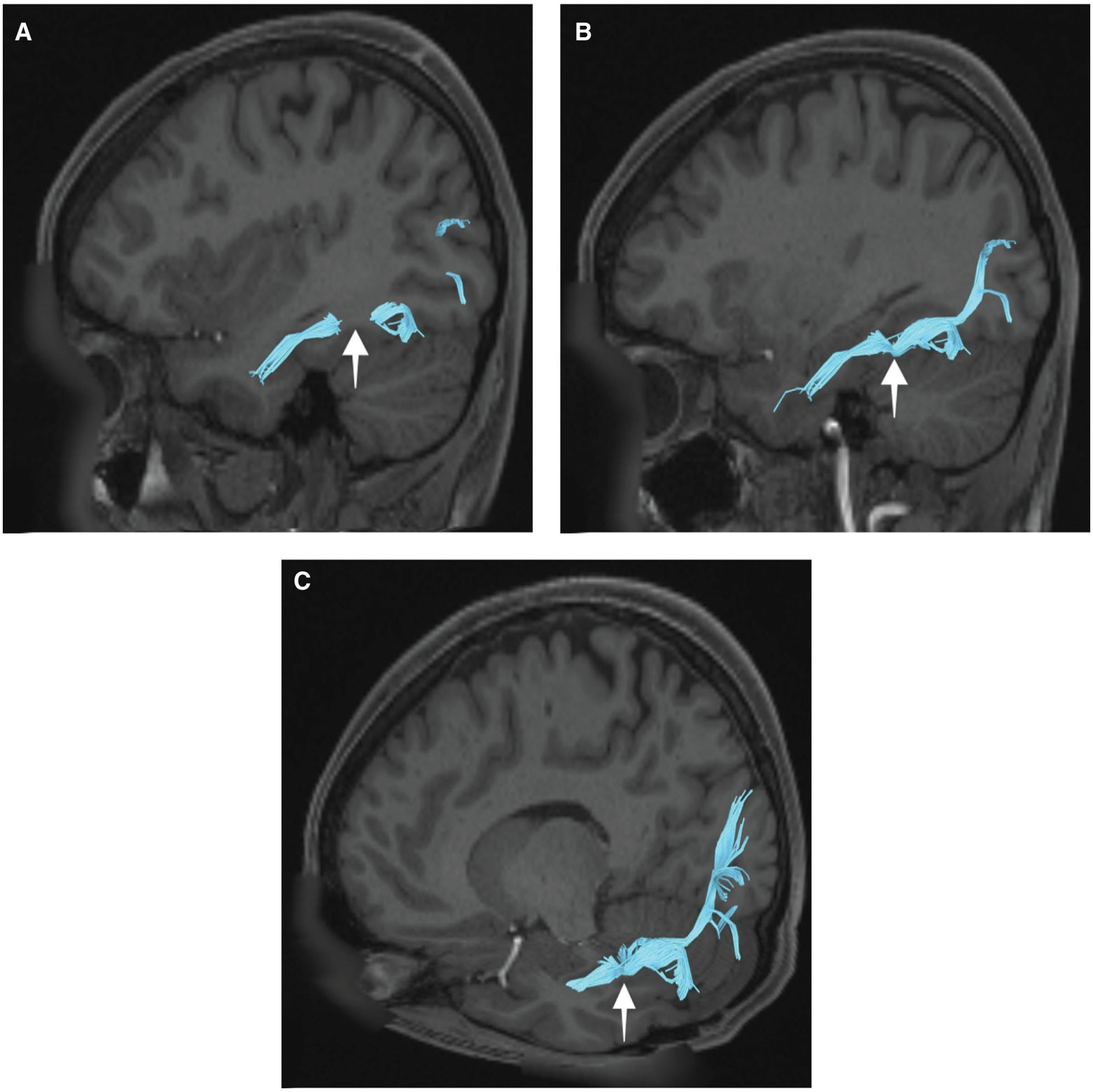

FIGURE 46. *Structural connectivity of PHA2 in the left hemisphere, shown on T1-weighted MR images.* **A** *to* **C**, *Three sagittal views from* **A**, *most lateral to* **B**, *and* **C**, *most medial showing projections to the inferior temporal lobe and the occipital lobe. Light blue: white matter tracts of PHA2 demonstrating connections with the ILF.*

language production. However, a good place to begin answering this question is to look at likely hub sites. As a graph theory term, we cannot be certain which are the hubs, but based on our work, two plausible candidates are STSvp and PHT. We base that statement on their extensive degree of functional connectivity to multiple widespread brain regions suggesting their role as an outflow site of these areas, their functional connectivity maps that straddle both clusters of sites in the region, their location near gross anatomic areas where we and others have commonly found language sites during awake brain surgery, and the presence of direct connections uniting these areas with the relevant areas typically associated with language production cortices, namely areas 44 and 6r. These seem like good candidates for the hubs of the language network. However, this needs

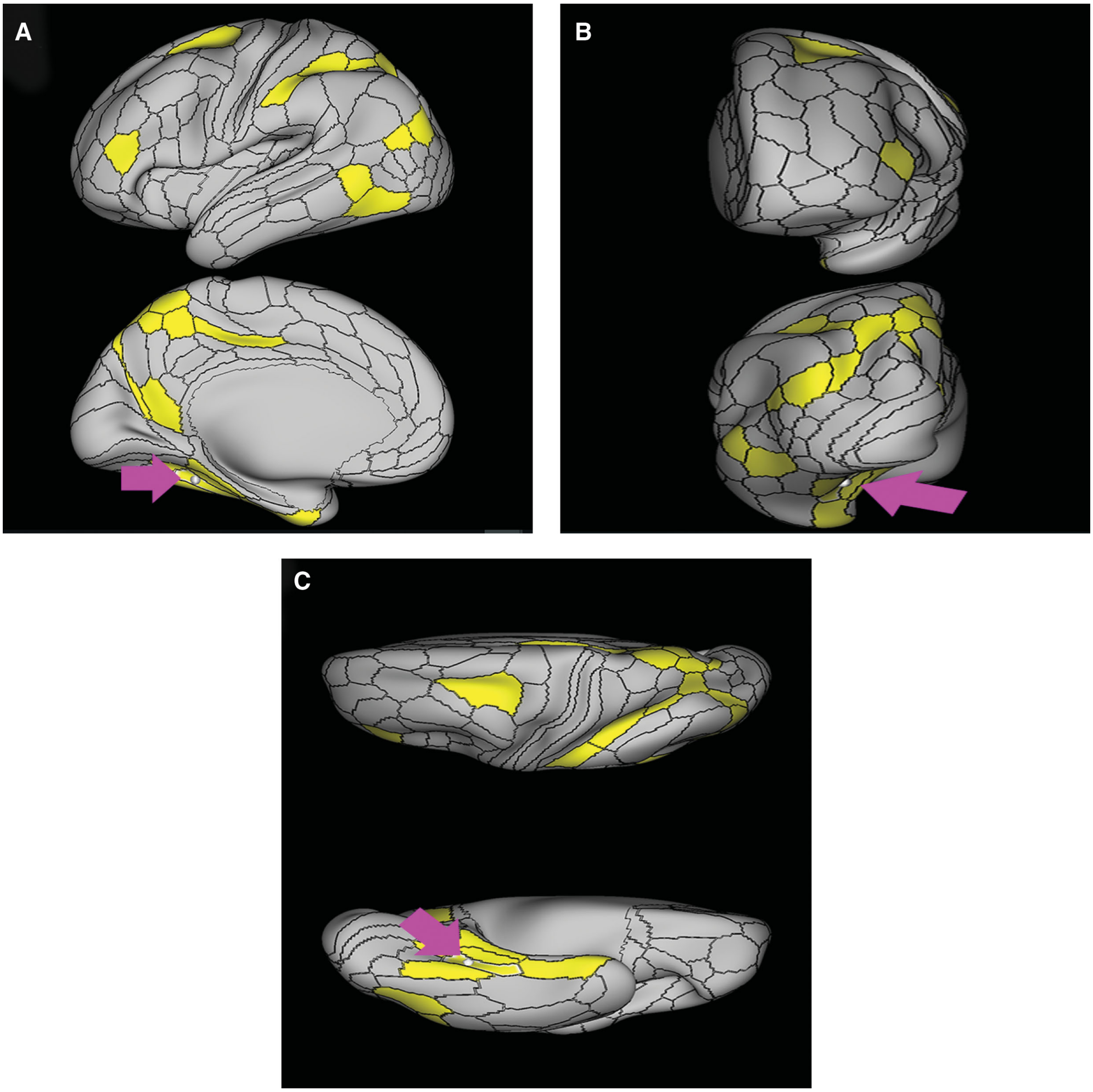

FIGURE 47. *Functional connectivity of PHA3 demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation of interest.*

more formal testing with other methods and repetition in other datasets.

The Polar Temporal System

The polar areas, most prominently TGd, form a junction point for three systems of tracts. They include the end point of the ILF, the SLF/arcuate system, and the uncinate fasciculus. Area TGd receives fibers from all three systems, and has some aspects of hubness including functional connections to diverse brain regions such as the frontal opercula and parietal lobe. It is also functionally linked to the lateral temporal areas. However, its exact functional role requires more study as it is not immediately obvious what modules or subnetworks it serves to link. Functionally, it stands to bridge auditory, semantic, visual, and paralimbic cortices; however, it is not immediately obvious to us what this means.

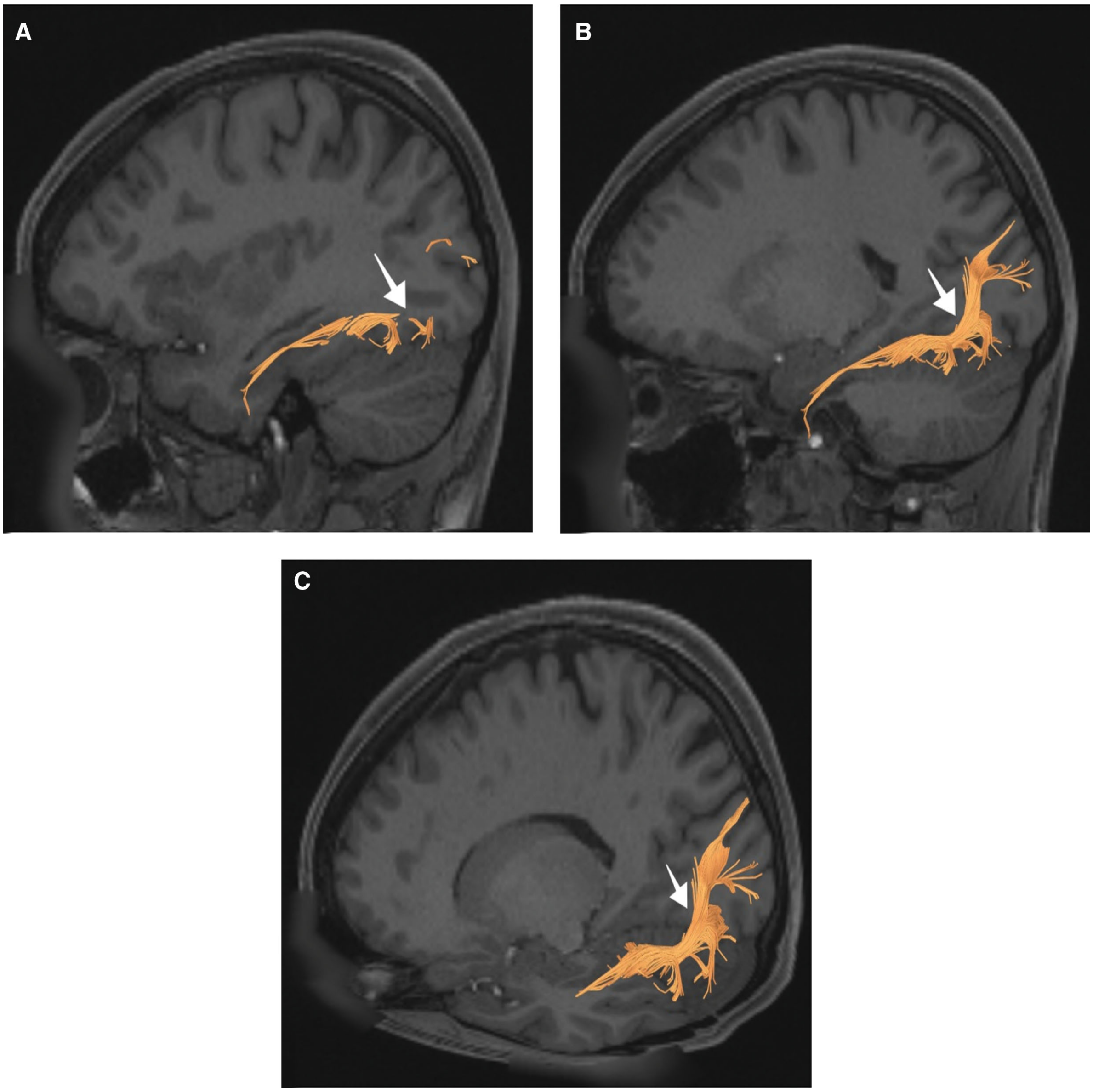

FIGURE 48. *Structural connectivity of PHA3 in the left hemisphere, shown on T1-weighted MR images.* **A-C**, *Three sagittal views from* **A**, *most lateral to* **B**, *and* **C**, *most medial showing projections to the inferior temporal lobe and the occipital lobe. Light orange: white matter tracts of PHA3 demonstrating connections with the ILF.*

The Inferior Temporal System

The inferior temporal lobe has not been an intense area of study in neurosurgery due to its relative tolerance to manipulation, and its inaccessibility during awake brain surgery. Thus, many of us would struggle to define precisely what this part of the brain does. The most obvious answer based on this work is that it plays some role in the cognitive and memory-related aspects of visual processing.[1,7] We base this idea on the literature role for these areas and their extensive connections to visual areas via the ILF. This obviously deserves greater attention given the frequency with which these areas are manipulated in clinical practice.

The Medial Temporal System

As this aspect of temporal lobe anatomy is probably the most familiar to our group, we were surprised at the complexity of the structural and functional connectivity of the parahippocampal cortices. In short, we found that these areas formed a module of types, with areas like EC having primarily local connections to other members of the group. The connectivity of areas like PreS and PHA3 to the posterior cingulate areas was also expected based on descriptions of the anatomy in the literature.[18,19] What was unexpected is how these areas are densely interconnected with visual association areas. For example, in addition to its connections to the ventral posterior cingulate areas, PreS has functional and structural connections to several early visual areas, as well as POS1 and POS2, which are mostly visually linked areas in the parieto-occipital sulcus. The PHA areas are also linked closely to the neighboring VMV areas posteriorly, and PHA3 shows connectivity to early visual areas. We found that these findings correlated well with other reports suggesting that, for example, PHA3 is involved in complex scene processing.[15] While this is not entirely new in the literature, to our knowledge this has not been fully appreciated in the neurosurgical literature.

How does Visual Information Reach the Semantic Areas, and how is it Processed by the Language System?

This is the critical question, and the answer is less clear to us now that we have a detailed wiring diagram of the area. This is not a trivial point, as loss of visual input to the semantic areas in the posterior temporal lobe on the left is the likely mechanism of anomia and possibly of allocentric neglect on the right side. The dissociation of primary progressive nonfluent aphasia from semantic dementia (the latter being linked to the temporal lobe in cases of frontotemporal dementia by atrophy patterns) strongly argues for a temporal location for the semantic stream.[20] Given the frequent finding of anomia sites during stimulation in the inferior subinsular region (where IFOF is running), we and others have suggested that IFOF may be the key pathway for semantic and visual knowledge to access the language processing regions.[21,22] However, given that we have found no evidence that any part of the ventral stream, lateral occipital lobe, or temporal lobe contributes substantially to IFOF, it is hard to postulate that the direct connections of IFOF between areas 45 and MIP or V7 really are the contributors to semantic knowledge being processed by the speech motor system. Given the only connections we could find between the visual areas and the inferior frontal gyrus link parts of area 47 to early visual areas like V1 through V4, the role of IFOF is not very obvious to us. It is conceivable that somehow some tracts course along with IFOF from the semantic regions, but we have not found evidence of this. While deterministic tractography may not constitute small tracts crossing each other or making sharp angles, it is difficult to imagine that such a substantial pathway would be traveling in a fiber bundle this small given the large number of crossing fiber bundles our methodology can differentiate. It is best to say at least that this is not obviously the answer, and other ideas should be entertained.

There are several other possible mechanisms by which visual information can access the semantic areas. The most obvious candidate lies in the observation that FST and PH, which seem to be hubs in the lateral occipital visual processing system, are immediately adjacent to PHT, which has hub-like qualities in the lateral temporal system. Alternately, all of these areas give fibers to the SLF/arcuate system, and it is possible they can influence language or other relevant functions directly in some form. One challenge to this idea is the observation that penetrating the lateral occipital lobe generally does not lead to anomia in our experience. The classic alexia-without-agraphia model suggests that contralateral fibers crossing through the splenium are able to compensate for this loss;[23] however, our methods are not able to delineate these fibers accurately.

Alternate pathways include the ILF fibers passing through the temporal lobe, though none of these fibers enter areas classically associated with language or semantic function, and we have not found that removing areas of the temporal lobe that correspond with TF or TGd cause anomia or language problems. Also worth considering is the occipitotemporal pathway, which is series of u-fiber connections in the inferolateral temporal and occipital lobes.[24] We have noted alexia sites in this general position, but have not noted anomia.

It remains unclear what the relationship is between the semantic language areas of the posterior temporal lobe. More specifically, it is unclear how information first gets from the visual system to the semantic areas, how the brain compensates for the loss of ipsilateral visual input so long as the contralateral side is available to these areas, and how this information accesses the language motor system. While these gaps in our knowledge may be limitations of the tractography methods, it is worth considering the idea that the connections via the IFOF may not be the true pathway for semantic information flow.

Disclosures

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