A Connectomic Atlas of the Human Cerebrum—Chapter 9: The Occipital Lobe

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In this supplement, we build on work previously published under the Human Connectome Project. Specifically, we seek to 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 9, we specifically address regions relevant to the occipital lobe and the visual system.

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

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The occipital lobe is well known as the seat of vision and visual processing, and this section focuses on the lobe as a unit for this reason. Despite this seeming simplicity, vision is a highly complex sense, and visual processing is known to involve numerous hierarchical regions and parallel processing streams, in addition to top-down and bottom-up regulation from numerous areas. The large number of small subregions in this section attests to its complexity. As a result, the occipital lobe is quite difficult to study, despite the general paucity of sulcal landmarks. Further, several of these areas are in awkward positions, for example some straddle the interhemispheric cleft. As such, neurosurgical anatomy of the visual system generally focuses on the primary visual system, and less on secondary visual areas, which are much harder to incorporate into our thinking. This section attempts to make further inroads into the exact anatomy of the visual system, with the acknowledgement that this remains one of the more complex systems in the cerebrum.

ABBREVIATIONS: FFC, fusiform face complex; **FM,** forceps major; **IFOF,** inferior fronto-occipital fasciculus; **ILF,** inferior longitudinal fasciculus; **LO1,** lateral occipital 1; **LO2,** lateral occipital 2; **LO3,** lateral occipital 3; **MdLF,** middle longitudinal fasciculus; **MR,** magnetic resonance; **MST,** medial superior temporal area; **MT,** middle temporal; **OR,** optic radiations; **PIT,** posterior infratemporal cortex; **VMV1,** ventromedial visual area 1; **VMV2,** ventromedial visual area 2; **VMV3,** ventromedial visual complex 3; **VVC,** ventral visual complex

BASIC ORGANIZATION OF THE OCCIPITAL LOBE

Anatomically, the occipital lobe has generally been thought of as a three-sided pyramid with its apex at the occipital pole. The sides can roughly be described as follows:

Medial surface: well-defined regions, including the cuneus and lingual.

Basal surface: usually defined, including the occipito-temporal sulcus and collateral sulcus that extend along the anterior–posterior extent of the basal surface.

Lateral surface: inconsistent patterns of sulci that differ between individuals.

While this general way of thinking about the lobe is visually verifiable, it is not entirely functionally useful. We would propose that a more useful way of characterizing occipital lobe function is as a four-sided pyramid, with a parallelogram base, meaning that the superior surface is substantially smaller than the inferior (basal) surface. The additional superior surface involves the portion of occipital lobe where the convexity cortex spills onto the interhemispheric surface. In this description, functional areas segregate between the surfaces as follows:

Medial surface: primary visual areas (V1-V4).

Inferior (basal) surface: ventral visual stream (The "what" pathway).

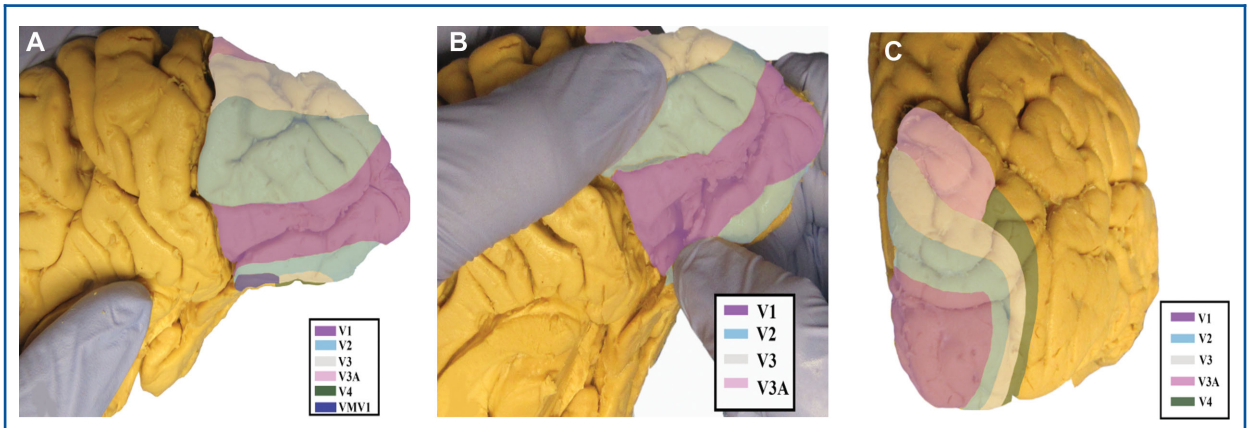

FIGURE 1. *Anatomic location of medial occipital lobe parcellations shown on the right hemisphere of a cadaver brain.* **A**, *Medial view of the occipital lobe.* **B**, *Medial view with widening of the calcarine sulcus to show extension of V1.* **C**, *Caudal view of the occipital pole. Corresponding labels are shown in the lower right corner of each figure.*

Superior surface: dorsal visual stream (the "where" pathway).
Lateral surface: Higher order visual processing areas.

Medial Surface

Nearly the entire medial surface of the occipital lobe is dedicated to the early visual areas V1, V2, V3, and V4. The primary visual area (V1) occupies the calcarine sulcus, and each subsequent area forms a C-shaped outer rim around the previous area. These areas are not entirely located on the medial surface, as the apex of the "C" spills onto the lateral surface before the open limb of the "C" spills back onto the medial surface both superiorly and inferiorly. The anatomic location of these parcellations is shown in Figure 1. This region has consistent white matter connections with the inferior fronto-occipital fasciculus (IFOF), middle longitudinal fasciculus (MdLF), inferior longitudinal fasciculus (ILF), and forceps major (FM). The combined tractography of V1, V2, V3, and V4 is shown in Figure 2.

Area V1

Where is it? Area V1 (visual area 1) is the primary visual cortex, which is located on the banks of the calcarine sulcus. It fills both banks of the sulcus and extends onto the tip of the occipital pole.

What are its borders? Area V1 borders V2 along its entire length. Its anterior border is with the prostriate cortex.

What is its functional connectivity? Area V1 demonstrates functional connectivity to areas SCEF and FEF in the premotor region, areas 46, 9-46d, p9-46v, 23c, 5mv, a24prime, p32prime, a32prime, and p24 in the frontal lobe, areas FOP4, FOP5, AVI, PoI1, 43, LBelt, PBelt, and A1 in the insula and opercular region, area PHT in the temporal lobe, areas 7am, 7PL, PGp, PFop, PF, MIP, LIPd, LIPv, IPS1, IP1, IP0, POS2, RSC, PCV, and DVT in the parietal lobe, areas ProS, V2, V3, and V4 in the medial occipital lobe, areas V3a, V3b, V7, V6, and V6a of the dorsal visual stream, areas fusiform face complex (FFC), ventral visual complex (VVC), V8, posterior infratemporal cortex (PIT), ventromedial visual area 1 (VMV1), ventromedial visual area 2 (VMV2), and ventromedial visual complex 3 (VMV3) of the ventral visual stream, and areas V3cd, lateral occipital 1 (LO1), lateral occipital 2 (LO2), lateral occipital 3 (LO3), PH, and FST of the lateral occipital lobe (Figure 3).

What are its white matter connections? Area V1 is structurally connected to the IFOF, MdLF, optic radiations (OR) and splenium of the corpus callosum. IFOF projections terminate at parcellations in the frontal pole including 11l, a10p, and p10p. Connections from the MdLF terminate in the superior temporal gyrus at STSda. There are consistent connections with FM to contralateral V1 through the splenium of the corpus callosum. Short association bundles are connected to V2, V3, and V3B (Figure 4).

What is known about its function? In each hemisphere, area V1 encodes an inverted, contralateral hemifield with greater cortical surface area devoted to visual stimuli detected by the fovea, indicating greater processing of input closer to the center of the visual field.[1] It has also been heavily implicated in the initial detection of motion, and signaling to the middle temporal area (MT) for the directional and spatial integration of global motion.[2]

Area V2

Where is it? Area V2 (visual area 2) is "C" shaped and wraps around V1. Its apex loops slightly around the occipital pole onto the lateral surface. Its upper limb is slightly shorter but makes up a large fraction of the cuneus. Its inferior limb makes up a large part of the lingula.

What are its borders? Area V2 wraps around V1 interiorly, and V3 makes up its external boundary. V6 and DVT make up the

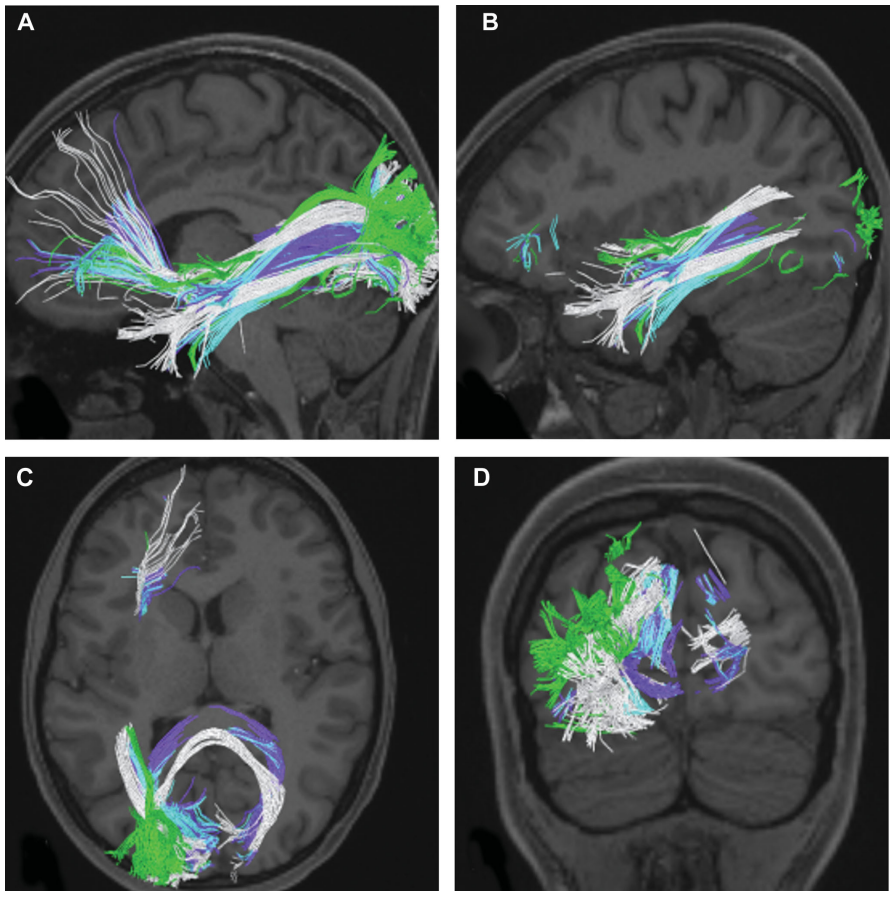

FIGURE 2. *Combined structural connectivity of medial surface parcellations.* **A**, *Medial and* **B**, *lateral views of sagittal plane,* **C**, *axial plane, and* **D**, *coronal plane are shown. Tracks include V1 (purple), V2 (light blue), V3 (white), and V4 (green).*

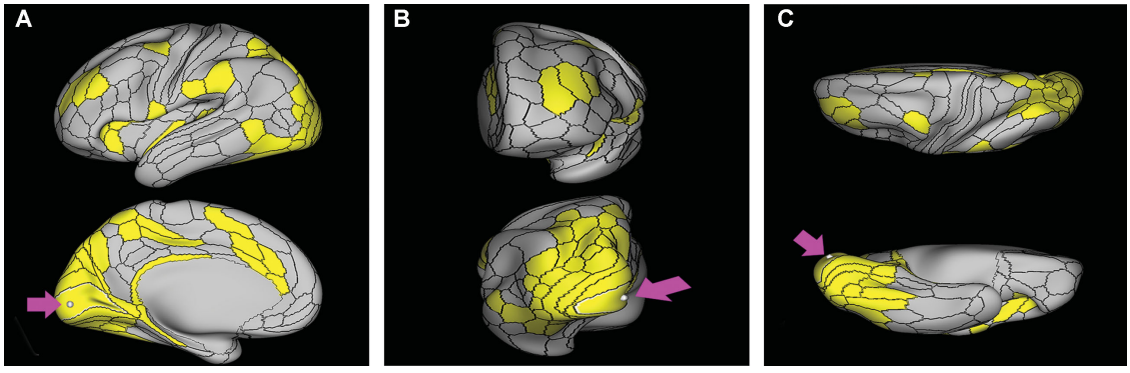

FIGURE 3. *Functional connectivity of V1 demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation of interest.*

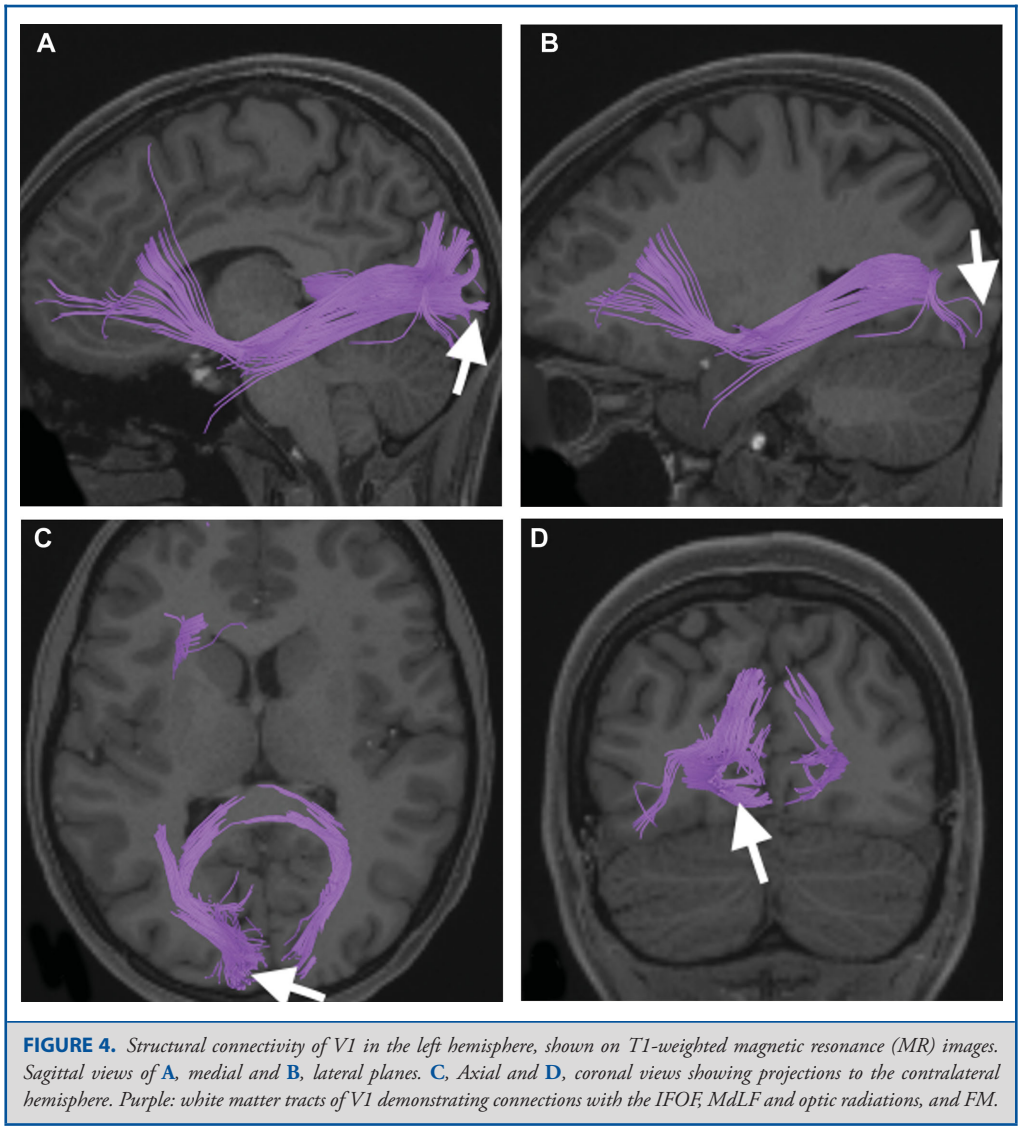

FIGURE 4. *Structural connectivity of V1 in the left hemisphere, shown on T1-weighted magnetic resonance (MR) images. Sagittal views of* **A**, *medial and* **B**, *lateral planes.* **C**, *Axial and* **D**, *coronal views showing projections to the contralateral hemisphere. Purple: white matter tracts of V1 demonstrating connections with the IFOF, MdLF and optic radiations, and FM.*

anterior border of its upper limb, and the anterior tip of its inferior limb forms a wedge between ProS and VMV1.

What is its functional connectivity? Area V2 demonstrates functional connectivity to areas 1, 2, 3a, 3b in the sensory strip, area 4 in the motor strip, areas SCEF, FEF, and 6a in the premotor region, areas 46, 9-46d, 23c, 5mv, 24dd, 24dv, a24prime, and p32prime in the frontal lobe, areas FOP3, FOP4, OP4, OP2-3, PoI1, PoI2, PFcm, 43, 52, RI, TA2, STV, PSL, MBelt, LBelt, PBelt, A1, and A4 in the insula and opercular region, area PHT in the temporal lobe, areas 7PC, PGp, PFop, AIP, VIP, MIP, LIPd, LIPv, IPS1, IP0, PCV, and DVT in the parietal lobe, areas ProS, V1, V3, and V4 in the medial occipital lobe, areas V3a, V3b, V7, V6, and V6a of the dorsal visual stream, areas FFC, VVC, V8, PIT, VMV1, VMV2, and VMV3 of the ventral visual stream, and areas TPOJ1, TPOJ2, TPOJ3, medial superior temporal area (MST), MT, V3cd, V4t, LO1, LO2, LO3, PH, and FST of the lateral occipital lobe (Figure 5).

What are its white matter connections? Area V2 is structurally connected to the IFOF, ILF, MdLF, and contralateral hemisphere. IFOF projections terminate at parcellations in the frontal pole including 8BL, 9a, 9p, 10d, 10pp, a10p, and 10pp. Connections from the MdLF terminate in the superior temporal gyrus at STSda, TGd, and TE1a. There are consistent connections with the FM to the contralateral hemisphere through the splenium of the corpus callosum that connect to V1, V2, V3, V4, V6, DVT, and V3A. Short association bundles are connected to V1, V2, V3, V4, V6, V3A, and DVT (Figure 6).

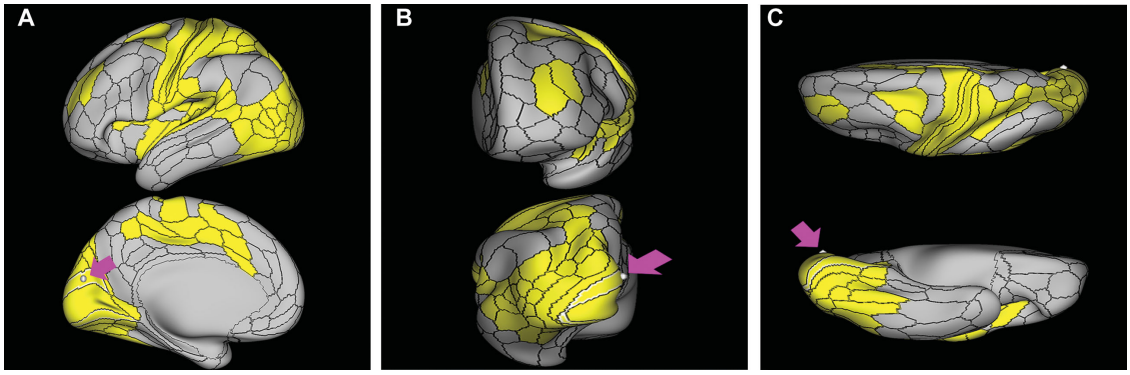

FIGURE 5. *Functional connectivity of V2 demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation of interest.*

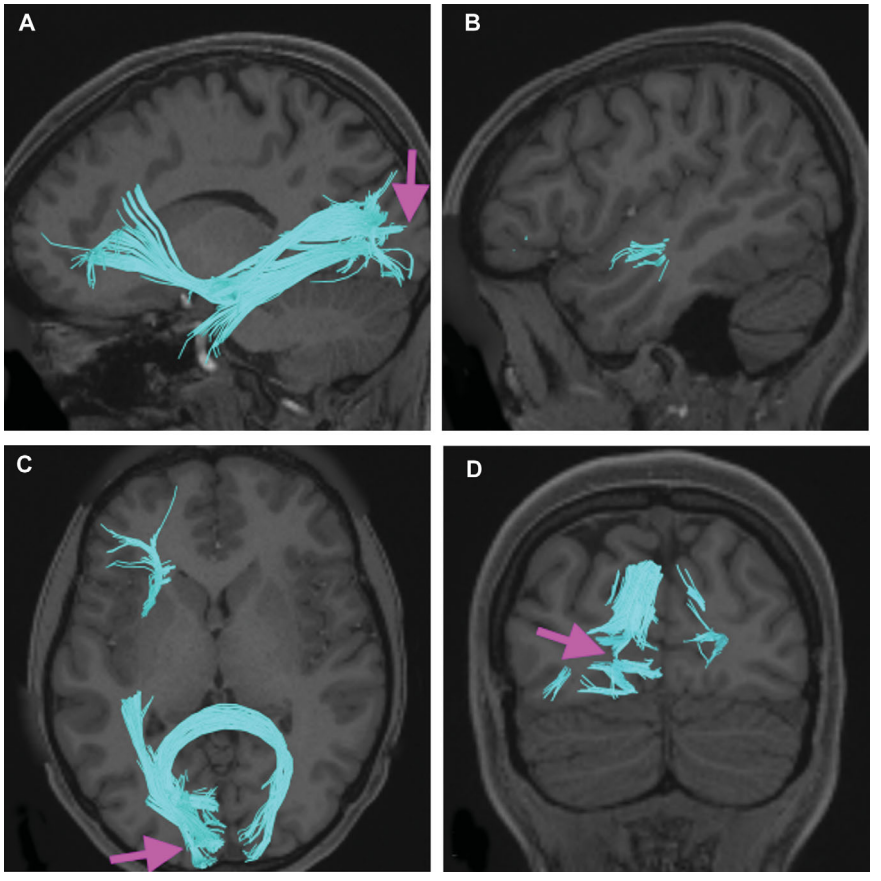

FIGURE 6. *Structural connectivity of V2 in the left hemisphere, shown on T1-weighted MR images. Sagittal views of* **A**, *medial and* **B**, *lateral planes.* **C**, *Axial and* **D**, *coronal views showing projections to the contralateral hemisphere. Light blue: white matter tracts of V2 demonstrating connections with the IFOF, ILF, MdLF, and contralateral hemisphere.*

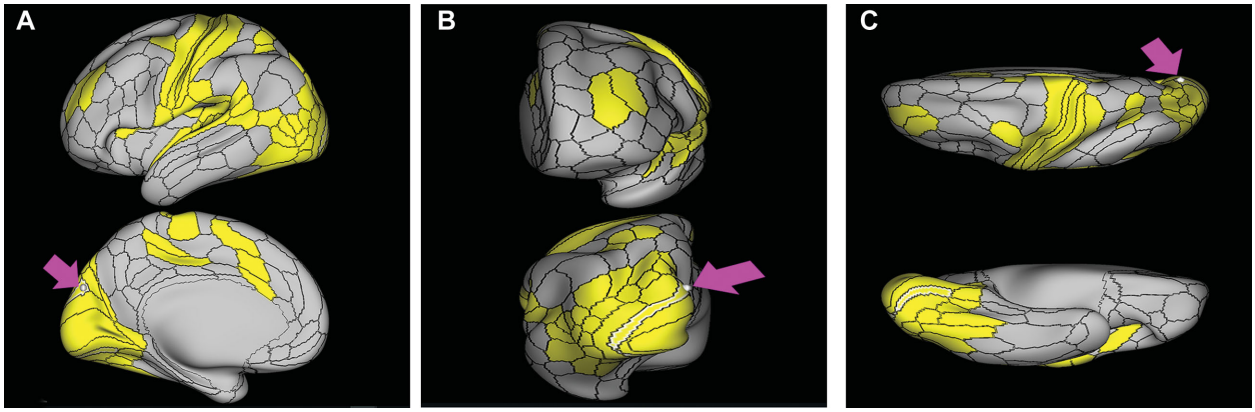

FIGURE 7. *Functional connectivity of V3 demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation of interest.*

What is known about its function? Area V2 partitions the visual field into two discontinuous, inverted, contralateral quarterfield maps divided by the horizontal meridian. V2 also perceives visual stimuli at greater angles from the foveal point than V1, indicating its perception of the visual field is farther from the fovea than V1.[1] Additionally, V2 has been implicated in more complex visual integration after receiving information from V1, most notably, the differentiation between stimulus and background.[3]

Area V3

Where is it? Area V3 (visual area 3) is "C" shaped and wraps around V2. Its apex loops around the occipital pole well onto the lateral surface. Its upper limb makes up a lesser fraction of the cuneus. Its inferior limb makes up the lower half of the lingula.

What are its borders? Area V3 wraps around V2 interiorly, and V4 makes up its external boundary. Its anterior limb has V3a as a superior boundary and V6 as an anterior boundary. Its inferior limb has VMV1 as an anterior boundary.

What is its functional connectivity? Area V3 demonstrates functional connectivity to areas 1, 2, 3a, 3b in the sensory strip, area 4 in the motor strip, areas SCEF, FEF, and 6a in the premotor region, areas 46, 9-46d, 23c, 5mv, a24prime, and p32prime in the frontal lobe, areas FOP3, FOP4, OP4, OP2-3, PoI1, PFcm, 43, 52, RI, TA2, STV, PSL, MBelt, LBelt, PBelt, A1, and A4 in the insula and opercular region, areas PGp, PFop, VIP, LIPd, LIPv, IPS1, IP0, and DVT in the parietal lobe, areas ProS, V1, V3, and V4 in the medial occipital lobe, areas V3a, V3b, V7, V6, and V6a of the dorsal visual stream, areas FFC, VVC, V8, PIT, VMV1, VMV2, and VMV3 of the ventral visual stream, and areas TPOJ1, TPOJ2, MST, MT, V3cd, V4t, LO1, LO2, LO3, PH, and FST of the lateral occipital lobe (Figure 7).

What are its white matter connections? Area V3 is structurally connected to the IFOF, ILF, MdLF, and FM. The IFOF projections originate from the superior portion of the parcellation before it curves inferiorly to the basal surface of the occipital lobe. Projections from the IFOF have typical anterior terminations that include 8BL, 9a, 9p, and 10s. Connections from the MdLF terminate at A5 of the superior temporal gyrus. ILF projections originate from the inferior portion of V3 along the basal surface of the occipital lobe and terminate at STGa and TGd. Contralateral connections with FM course through the splenium of the corpus callosum and terminate at V1 and V2. Short association bundles are connected to V1, V2, V3A, and V4 (Figure 8).

What is known about its function? Similar to V2, area V3 receives visual input as two discontinuous, inverted, contralateral quarterfield maps divided by the horizontal meridian. Area V3 perceives even wider degrees of the visual field than V2, indicating it perceives visual stimuli at an even further angle from the fovea than V2.[1] Additionally, area V3 (and in a more limited role, V2) has been shown to play a role in the perception and integration of global motion by processing directionally specific, visual, local motion in its broad receptive fields and transmitting information to area V6, and the dorsal visual stream for further processing.[2]

Area V4

Where is it? Area V4 (visual area 4) is "C" shaped and wraps around V3. It is primarily located on the posterior aspect of the lateral occipital surface. Its upper limb does not extend onto the medial surface as it's somewhat shorter than the corresponding limbs of V3 and V2. Its inferior limb extends onto the medial basal surface of the occipital lobe.

What are its borders? Area V4 borders V3 internally. Its superior limb ends in V3a and its inferior limb ends in VMV2 and VMV3. It shares an external border with a large number of visual

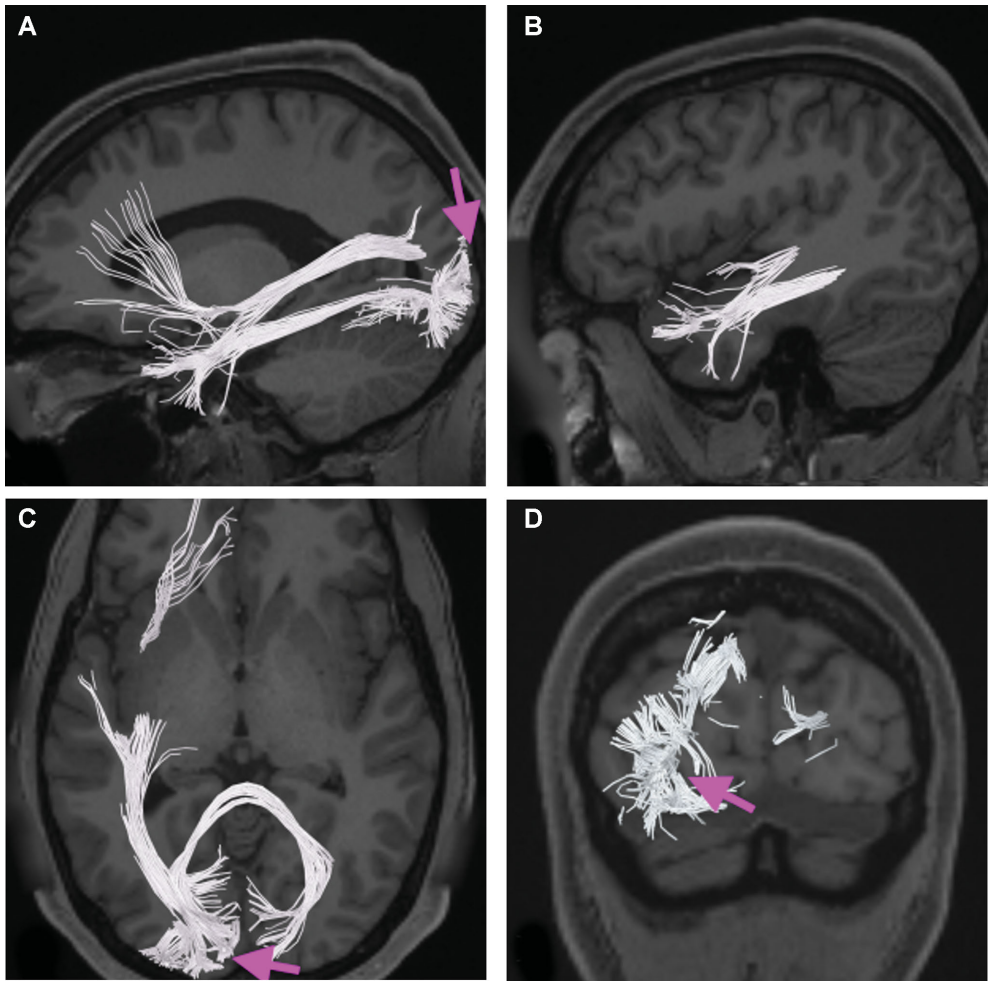

FIGURE 8. *Structural connectivity of V3 in the left hemisphere, shown on T1-weighted MR images. Sagittal views of* **A**, *medial and* **B**, *lateral planes.* **C**, *Axial and* **D**, *coronal views showing projections to the contralateral hemisphere. White: white matter tracts of V3 demonstrating connections with the IFOF, ILF, MdLF, and FM.*

processing areas. From superior to inferior these are: V3b, V3cd, LO1, LO2, Pit, and V8.

What is its functional connectivity? Area V4 demonstrates functional connectivity to areas 1, 3a, 3b in the sensory strip, area 4 in the motor strip, areas SCEF, FEF, and 6a in the premotor region, areas 9-46d, 23c, a24prime, and p32prime in the frontal lobe, areas FOP3, OP4, PFcm, 43, 52, RI, TA2, STV, PSL, MBelt, LBelt, PBelt, A1, and A4 in the insula and opercular region, areas PFop, VIP, LIPv, IPS1, IP0, and DVT in the parietal lobe, areas ProS, V1, V3, and V4 in the medial occipital lobe, areas V3a, V3b, V7, V6, and V6a of the dorsal visual stream, areas FFC, VVC, V8, PIT, VMV1, VMV2, and VMV3 of the ventral visual stream, and areas TPOJ1, MST, MT, V3cd, V4t, LO1, LO2, LO3, PH, and FST of the lateral occipital lobe (Figure 9).

What are its white matter connections? Area V4 is structurally connected with the ILF, MdLF, and portions of the IFOF. ILF projections terminate at TF. IFOF projections are inconsistent and the parcellations at which this tract terminates are unable to be discerned. MdLF connections terminate at the superior temporal gyrus at A4 and A5. Short association bundles are connected to V3, V3A, V3B, V3CD, LO1, LO2, and V6A (Figure 10).

What is known about its function? Area V4 has been shown to encode texture, patterns, form, and color perception, making it integral to object and pattern recognition.[4] Interestingly, the literature has also implicated V4 in the perception of contralateral, hemifield representations of the peripheral visual field.[5]

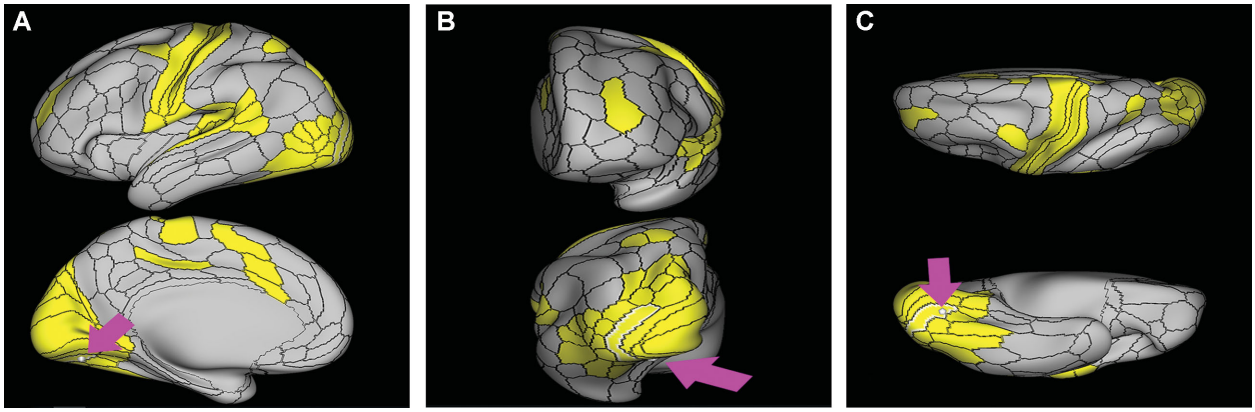

FIGURE 9. *Functional connectivity of V4 demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation of interest.*

Basal Occipital Areas

The basal occipital areas comprise parcellations V8, PIT, FFC, VVC, VMV1, VMV2, and VMV3 (Figure 11). This area has consistent white matter connections with the ILF and ventral occipital fasciculus (VOF). VMV2 also connects with the IFOF. The combined tractography of the parcellations is shown in Figure 12.

Area V8

Where is it? Area V8 (visual area 8) is found at the far posterior most portion of the fusiform gyrus.

What are its borders? Area V8 borders shares its entire medial and posterior border with V4. Its anteromedial border is with VMV3, its anterior border is with VVC, and anterolateral border is with FFC, which also forms some of its lateral border. PIT forms its posterolateral border.

What is its functional connectivity? Area V8 demonstrates functional connectivity to area FEF in the premotor region, areas 43, PBelt, and A4 in the insula and opercular region, areas VIP, LIPv, IPS1, IP0, and DVT in the parietal lobe, areas ProS, V1, V2, V3, and V4 in the medial occipital lobe, areas V3a, V3b, V7, V6, and V6a of the dorsal visual stream, areas VVC, V8, VMV2, and VMV3 of the ventral visual stream, and areas V3cd, LO1, LO3, PH, and FST of the lateral occipital lobe (Figure 13).

What are its white matter connections? Area V8 is structurally connected with the ILF and VOF. The ILF terminates at TGv but the connections with this tract are inconsistent across brains. The VOF tract courses mediodorsal from V8 to terminate at V3a, V3b, V3cd, and V7. Short association bundles are connected to V4, PIT, FFC, and V3 (Figure 14).

What is known about its function? Area V8 is most notably responsible for the perception and processing of color in the visual field.[6]

Area PIT

Where is it? Area PIT is found posterior most portion of the occipitotemporal gyrus where it begins to blend into the occipital pole. It spills slightly onto the lateral surface.

What are its borders? Area PIT borders V8 and V4 medially. V4 also forms its posterior boundary. It borders FFC and PH anteriorly. LO2 is its superior (lateral) neighbor.

What is its functional connectivity? Area PIT demonstrates functional connectivity to area FEF in the premotor region, areas PBelt, and A4 in the insula and opercular region, areas VIP, LIPv, IPS1, and DVT in the parietal lobe, areas V1, V2, V3, and V4 in the medial occipital lobe, areas V3a, V3b, V7, V6, and V6a of the dorsal visual stream, areas VVC, FFC, V8 of the ventral visual stream, and areas V3cd, V4t, LO1, LO2, LO3, PH, MST, and FST of the lateral occipital lobe (Figure 15).

What are its white matter connections? Area PIT is structurally connected to VOF and its surrounding parcellations. VOF connections project mediodorsally to terminate at V3, V2, and V3a. Short association bundles are connected to PH, V8, V4, and V1 (Figure 16).

What is known about its function? Area PIT has been implicated in the analysis of the basic characteristics of color, such as hue, saturation, and brightness based on information provided by V8.[7]

Area FFC

Where is it? Area FFC is found in the posterior fusiform gyrus. It comprises the lateral half of the posterior portion of the gyrus

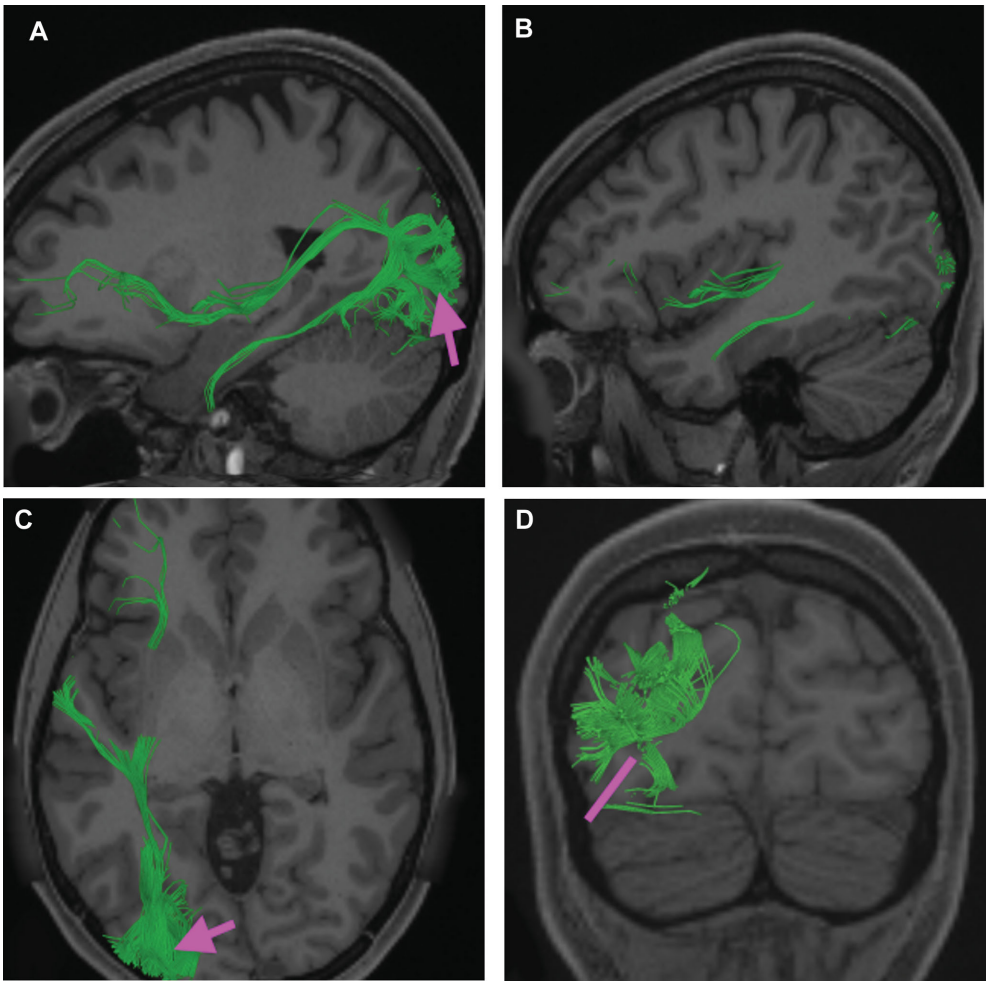

FIGURE 10. *Structural connectivity of V4 in the left hemisphere, shown on T1-weighted MR images. Sagittal views of* **A**, *medial and* **B**, *lateral planes.* **C**, *Axial and* **D**, *coronal views showing projections to the contralateral hemisphere. Green: white matter tracts of V4 demonstrating connections with the ILF, MdLF, and portions of IFOF.*

and forms the medial bank of the adjacent portion of the occipitotemporal sulcus.

What are its borders? Area FFC borders TF anteriorly, TE2p and PH laterally, and V8 and PIT posteriorly. VVC forms its medial boundary.

What is its functional connectivity? Area FFC demonstrates functional connectivity to areas 1,2, 3a, and 3b in the sensory strip, area 4 in the motor strip, areas SCEF, FEF, and 6v in the premotor region, areas OP4, STV, PFcm, 43, RI, LBelt, PBelt, A4, and A5 in the insula and opercular region, area TE2p in the temporal lobe, areas 7PC, PGp, PFt, AIP, MIP, VIP, LIPv, DVT, IP0, and IPS1 in the parietal lobe, areas V1, V2, V3, and V4 in the medial occipital lobe, areas V3a, V3b, V7, V6, and V6a of the dorsal visual stream, areas VVC, V8, PIT, VMV1, VMV2, and VMV3 of the ventral visual stream, and areas TPOJ1, TPOJ2, TPOJ3, V3cd, V4t, MT, LO1, LO2, LO3, MT, MST, PH, and FST of the lateral occipital lobe (Figure 17).

What are its white matter connections? Area FFC is structurally connected to the ILF. It also has many local U-fibers projecting from the parcellation. In some brains, fiber bundles connect with the SLF but this tract is inconsistent. The ILF projects toward the temporal pole and terminates at TGv. Short association bundles are connected to V4, PIT, LO3, FST, MST, MT, PH, and TPOJ2 (Figure 18).

What is known about its function? Area FFC is an information hub receiving extensive input from the ventral stream about

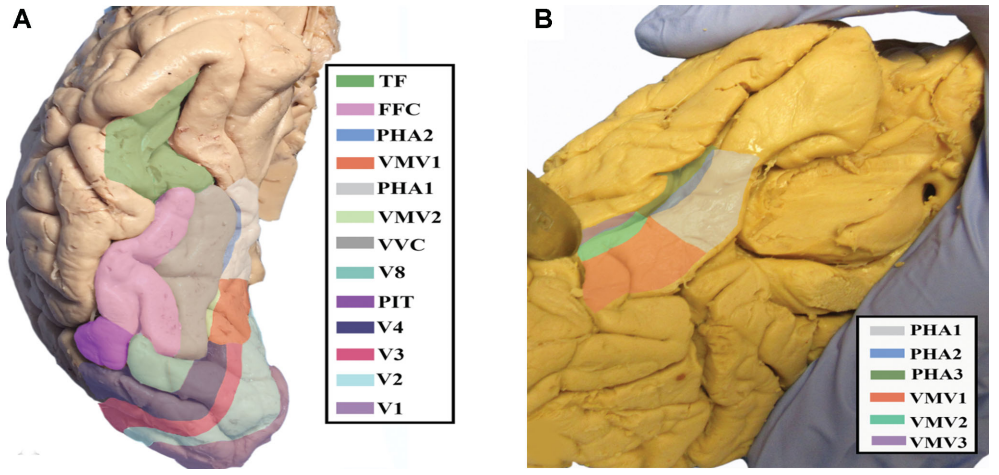

FIGURE 11. *Anatomic location of basal occipital lobe parcellations shown on the right hemisphere of a cadaver brain.* **A**, *Ventral view of the occipital lobe.* **B**, *Ventral view with widening of the collateral sulcus to show extension of VMV2, VMV3, PHA2, and PHA3. Corresponding labels are shown in the lower right corner of each figure.*

the static and dynamic details of invariant facial features and integrates them to produce the holistic form of a face. Using this information, area FFC plays an integral role in identity recognition and plays a minor role in emotional expression recognition due to its high activity for both neutral and expressive faces.[8,9]

Area VVC

Where is it? Area VVC is found in posterior fusiform gyrus where it makes up the medial half of this portion of the gyrus, as well as portions of the lateral bank of the collateral sulcus.

What are its borders? Area VVC borders TF anteriorly, FFC laterally, V8 posteriorly, and PHA3 and VMV3 medially.

What is its functional connectivity? Area VVC demonstrates functional connectivity to area FEF in the premotor region, areas PBelt and A4 in the insula and opercular region, areas VIP, LIPv, PGp, IPS1, IP0, and DVT in the parietal lobe, areas ProS, V1, V2, V3, and V4 in the medial occipital lobe, areas V3a, V3b, V7, V6, and V6a of the dorsal visual stream, areas VVC, V8, VMV2, and VMV3 of the ventral visual stream, and areas V3cd, MT, MST, V4t, LO1, LO2, LO3, PH, and FST of the lateral occipital lobe (Figure 19).

What are its white matter connections? Area VVC is structurally connected to the ILF and VOF. The ILF projects toward the temporal pole and terminates at TGv. The VOF lies orthogonal to the ILF and courses dorsomedially to end at V3b. Short association bundles are connected to FFC, PIT, V3B, V3CD, V8, VMV1, VMV2, and VMV3 (Figure 20).

What is known about its function? Area VVC has been heavily implicated in color perception in tandem with V4 and V8, and shows increased responsiveness to the detection of color in a monochromatic field, or the initial detection of color.[10] Additionally, area VVC is essential for the integration of color, contrast, and textural information for the recognition of places and recognition of a spatial map.[11]

Area VMV1

Where is it? Area VMV1 is found on the anteromedial lingula at the point where this gyrus blends anteriorly into the parahippocampal gyrus. It is located on the lower half of this portion of the gyrus.

What are its borders? Area VMV1 borders the inferior limb of V2 superiorly, the inferior limb of V3 posteriorly, VMV2 inferiorly, and PHA1 anteriorly. It may have some superior contact with ProS.

What is its functional connectivity? Area VMV1 demonstrates functional connectivity to area FEF in the premotor region, areas PHA1 in the temporal lobe, areas VIP, LIPv, IPS1, and DVT in the parietal lobe, areas V1, V2, V3, and V4 in the medial occipital lobe, areas V3a, V3b, V7, V6, and V6a of the dorsal visual stream, areas FFC, VVC, V8, VMV2, and VMV3 of the ventral visual stream, and areas V3cd, V4t, LO1, LO3, PH, and FST of the lateral occipital lobe (Figure 21).

What are its white matter connections? Area VMV1 is structurally connected with the ILF and VOF. The ILF projects to the temporal pole and terminates at TGd. The VOF lies orthogonal to the ILF and courses dorsomedially to V3a. Short association

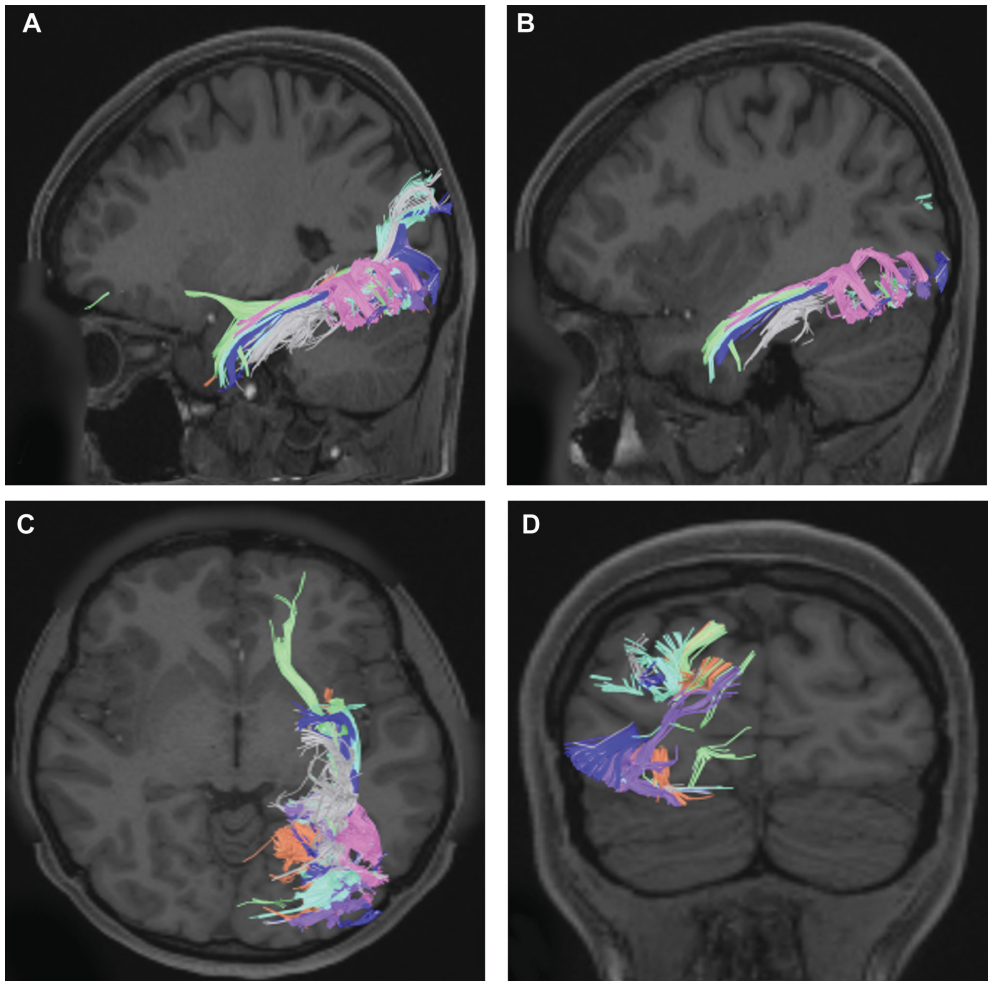

FIGURE 12. *Combined structural connectivity of basal surface parcellations.* **A**, *Medial and* **B**, *lateral views of sagittal plane,* **C**, *axial plane, and* **D**, *coronal plane are shown. Tracks include V8 (turquoise), PIT (dark blue), FFC (pink), VVC (gray), VMV1 (orange), VMV2 (light green), and VMV3 (purple).*

bundles are connected to V3A, V3, V6, V1, V8, and VMV3 (Figure 22).

What is known about its function? While area VMV1 is considered a new area, this region of the occipital lobe is suggested in the literature to be important for the integration of color, texture, and form information for the holistic recognition of places.[4,10,11]

Area VMV2

Where is it? Area VMV2 is found on the posterior superior bank of the collateral sulcus just as the lingula is blending with the parahippocampal gyrus anteriorly.

What are its borders? Area VMV2 borders V4 posteriorly, and PHA3 anteriorly. Its superior border is VMV1 and its inferior border is VMV3.

What is its functional connectivity? Area VMV2 demonstrates functional connectivity to area FEF in the premotor region, areas PHA3 in the temporal lobe, areas VIP, LIPv, PGp, IPS1, IP0, and DVT in the parietal lobe, areas ProS, V1, V2, V3, and V4 in the medial occipital lobe, areas V3a, V3b, V7, V6, and V6a of the dorsal visual stream, areas FFC, VVC, V8, VMV1, and VMV3 of the ventral visual stream, and areas V3cd, V4t, LO1, LO2, LO3, PH, and FST of the lateral occipital lobe (Figure 23).

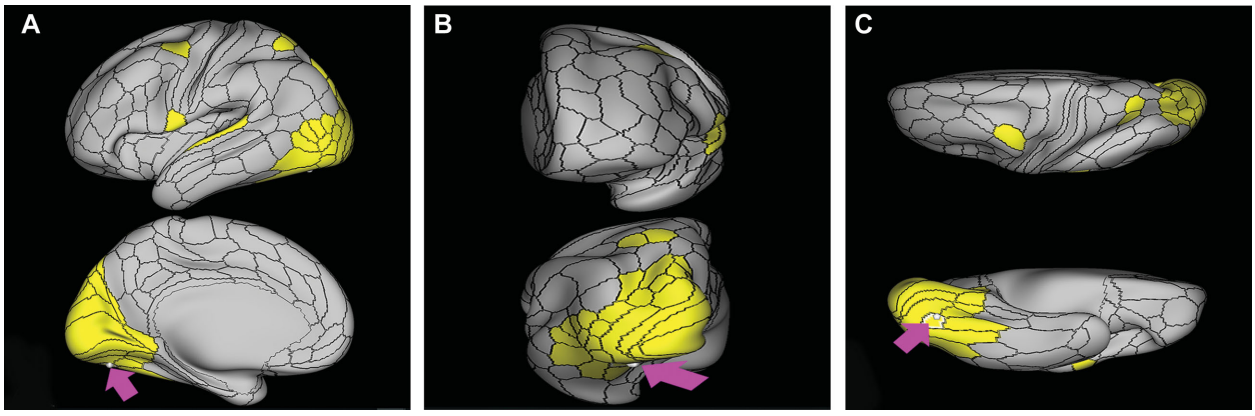

FIGURE 13. *Functional connectivity of V8 demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation of interest.*

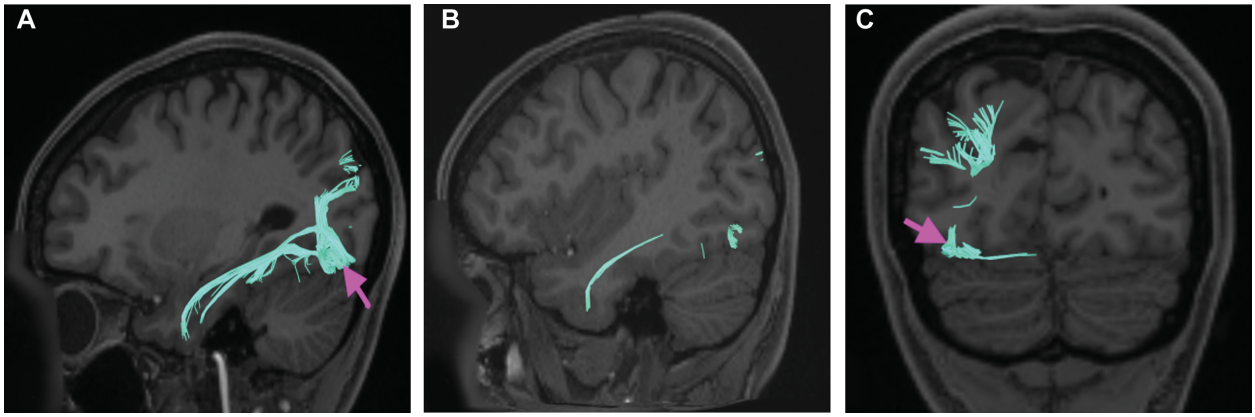

FIGURE 14. *Structural connectivity of V8 in the left hemisphere, shown on T1-weighted MR images. Sagittal views of* **A**, *medial and* **B**, *lateral planes, and* **C**, *coronal view showing. Turquoise: white matter tracts of V8 demonstrating connections with the ILF and VOF.*

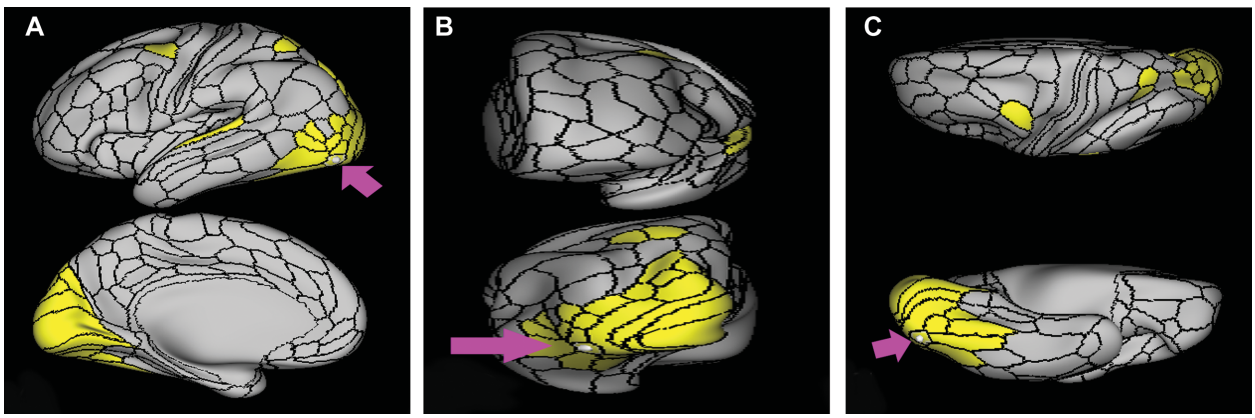

FIGURE 15. *Functional connectivity of PIT demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation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

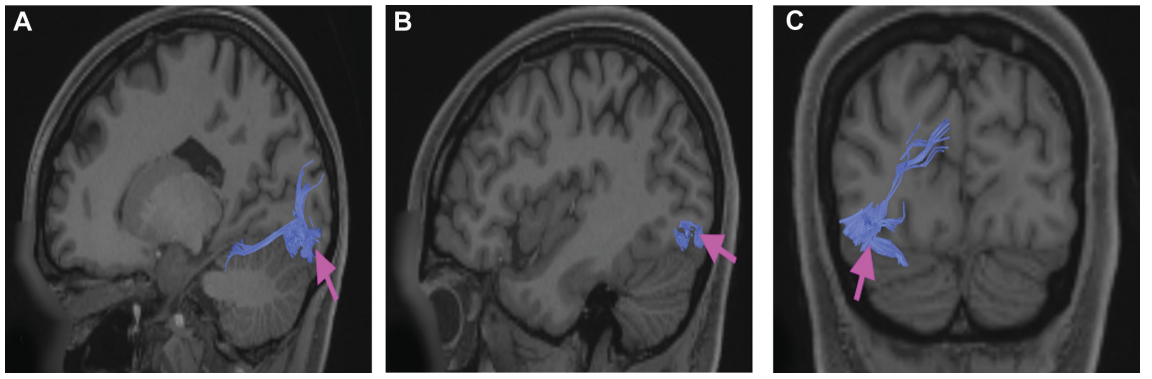

FIGURE 16. *Structural connectivity of PIT in the left hemisphere, shown on T1-weighted MR images. Sagittal views of* **A**, *medial and* **B**, *lateral planes, and* **C**, *coronal view showing. Dark blue: white matter tracts of PIT demonstrating connections with the VOF and its surrounding parcellations.*

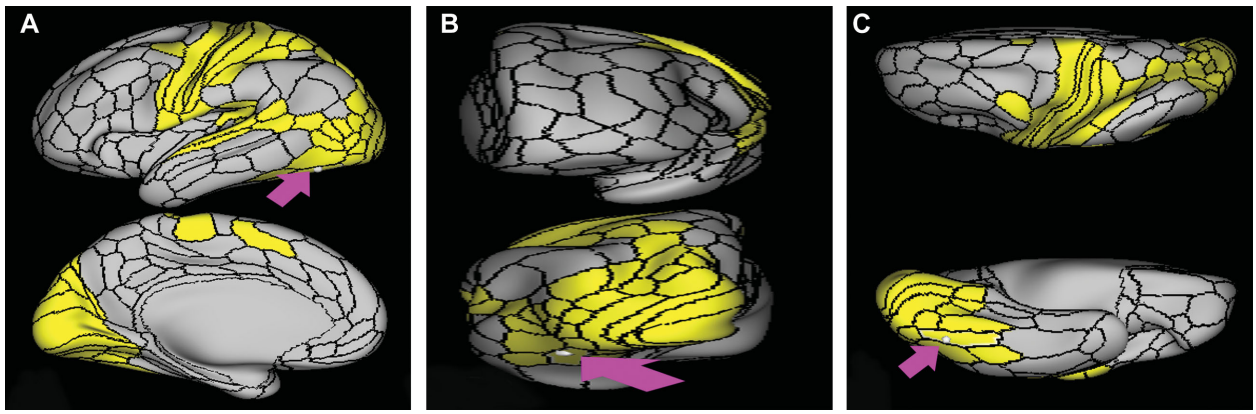

FIGURE 17. *Functional connectivity of FFC demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation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

What are its white matter connections? Area VMV2 is structurally connected with the ILF, IFOF, and VOF. The ILF courses through the temporal lobe to end at TGv. There are consistent tracts that run with the inferior portion of the IFOF and project to the pole of the frontal lobe. The VOF lies orthogonal to the ILF and ends at V3a. Short association bundles are connected to V1, V2, V3, V3A, V6A, FFC, and VVC (Figure 24).

What is known about its function? While area VMV2 is considered a new area, this region of the occipital lobe is suggested in the literature to be important for the integration of color, texture, and form information for the holistic recognition of places.[4,10,11]

Area VMV3

Where is it? Area VMV3 is found in the posterior most portion of the lateral bank of the collateral sulcus.

What are its borders? Area VMV3 borders the inferior limb of V4 and V8 posteriorly, and PHA3 anteriorly. Its superior (medial) border is VMV2, and its inferior (lateral) border is VVC.

What is its functional connectivity? Area VMV3 demonstrates functional connectivity to area FEF in the premotor region, areas PHA3 in the temporal lobe, areas VIP, LIPv, PGp, IPS1, IP0, and DVT in the parietal lobe, areas V1, V2, V3, and V4 in the medial occipital lobe, areas V3a, V3b, V7, V6, and V6a of the dorsal visual stream, areas FFC, PIT, VVC, V8, VMV2, and VMV3 of the ventral visual stream, and areas MT, MST, V3cd, V4t, LO1, LO2, LO3, PH, and FST of the lateral occipital lobe (Figure 25).

What are its white matter connections? Area VMV3 is structurally connected with the ILF and VOF. The ILF courses through the temporal lobe to terminate at PeEc. The VOF lies orthogonal to the ILF and projects dorsomedially to end at V3a and V3b.

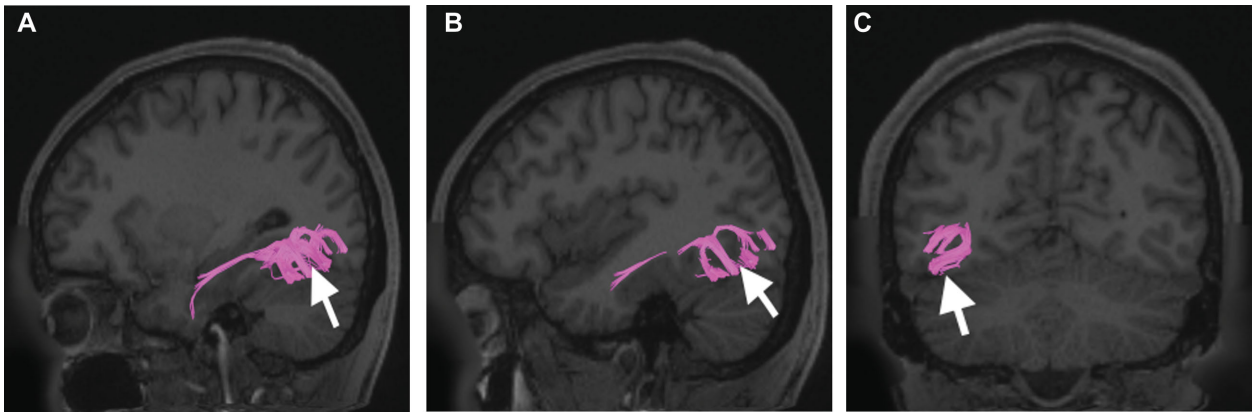

FIGURE 18. *Structural connectivity of FFC in the left hemisphere, shown on T1-weighted MR images. Sagittal views of* **A**, *medial and* **B**, *lateral planes, and* **C**, *coronal view showing. Pink: white matter tracts of FFC demonstrating connections with the ILF.*

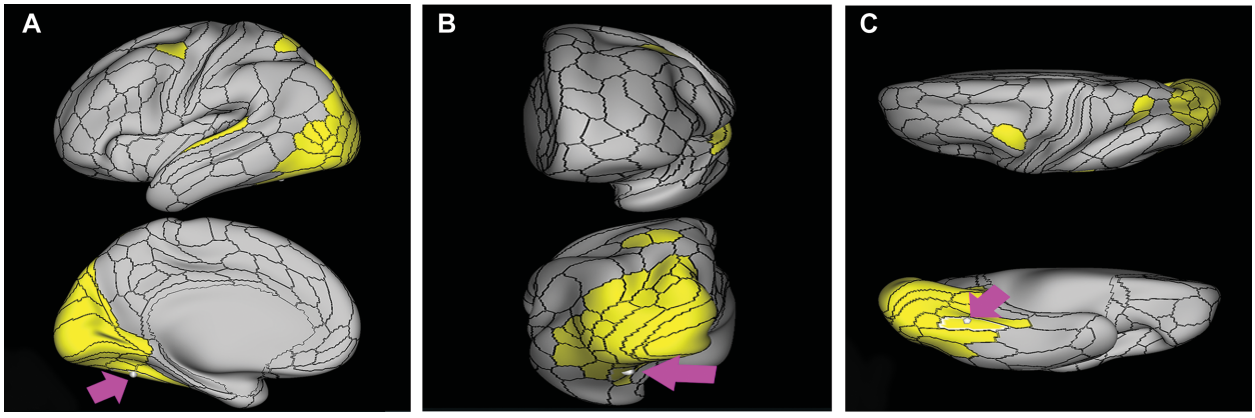

FIGURE 19. *Functional connectivity of VVC demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation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

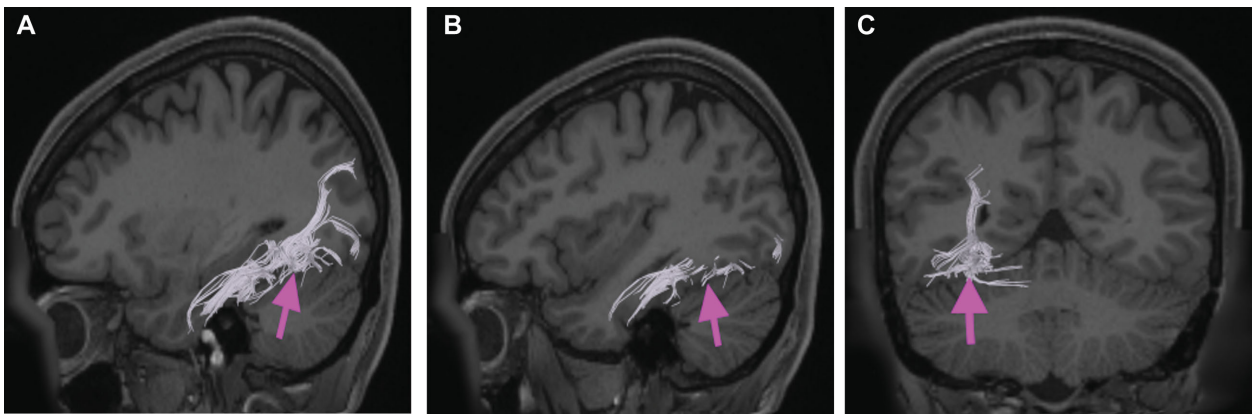

FIGURE 20. *Structural connectivity of VVC in the left hemisphere, shown on T1-weighted MR images. Sagittal views of* **A**, *medial and* **B**, *lateral planes, and* **C**, *coronal view showing. Gray: white matter tracts of VVC demonstrating connections with the ILF and VOF.*

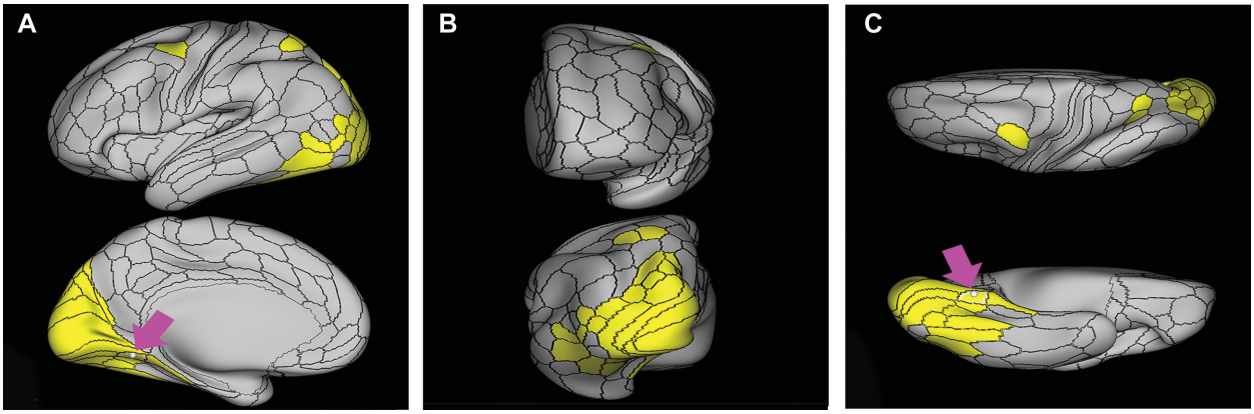

FIGURE 21. *Functional connectivity of VMV1 demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation of interest.*

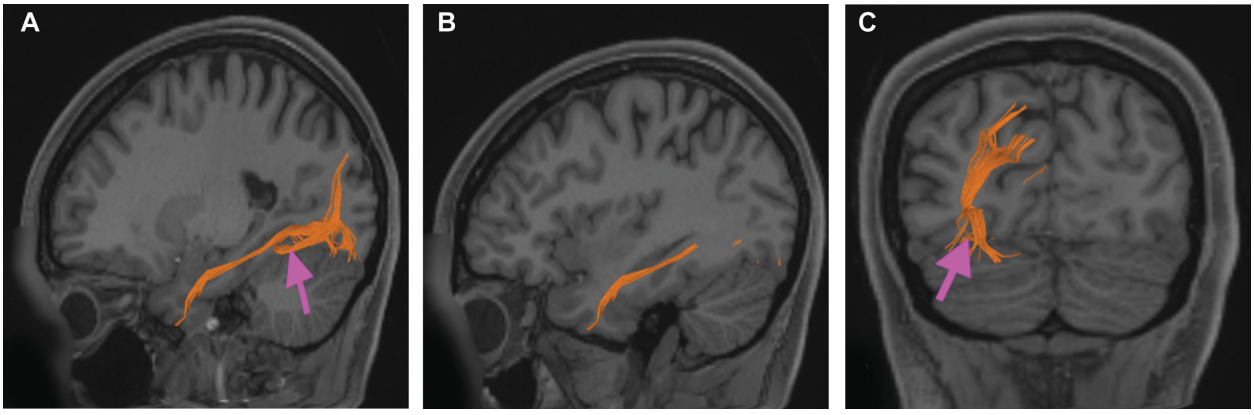

FIGURE 22. *Structural connectivity of VMV1 in the left hemisphere, shown on T1-weighted MR images. Sagittal views of* **A**, *medial and* **B**, *lateral planes, and* **C**, *coronal view showing. Orange: white matter tracts of VMV1 demonstrating connections with the ILF and VOF.*

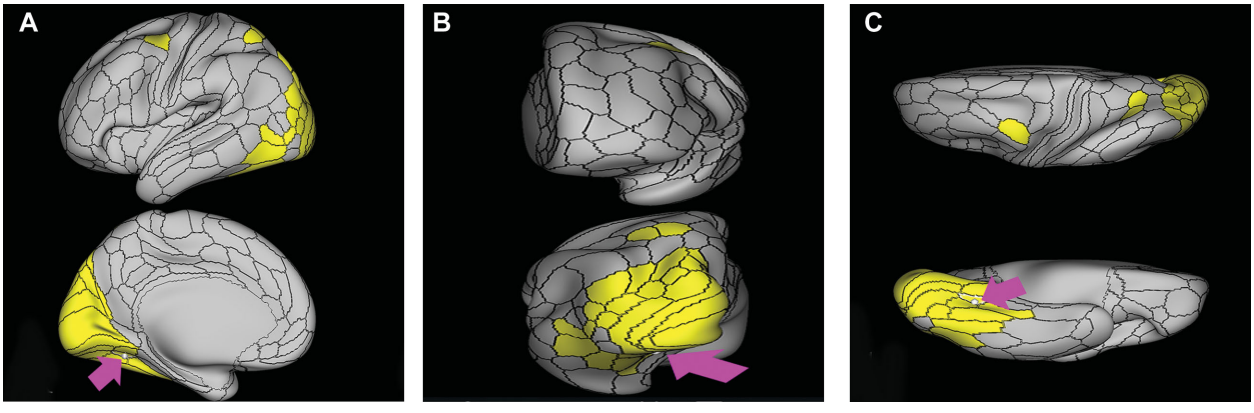

FIGURE 23. *Functional connectivity of VMV2 demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation of interest.*

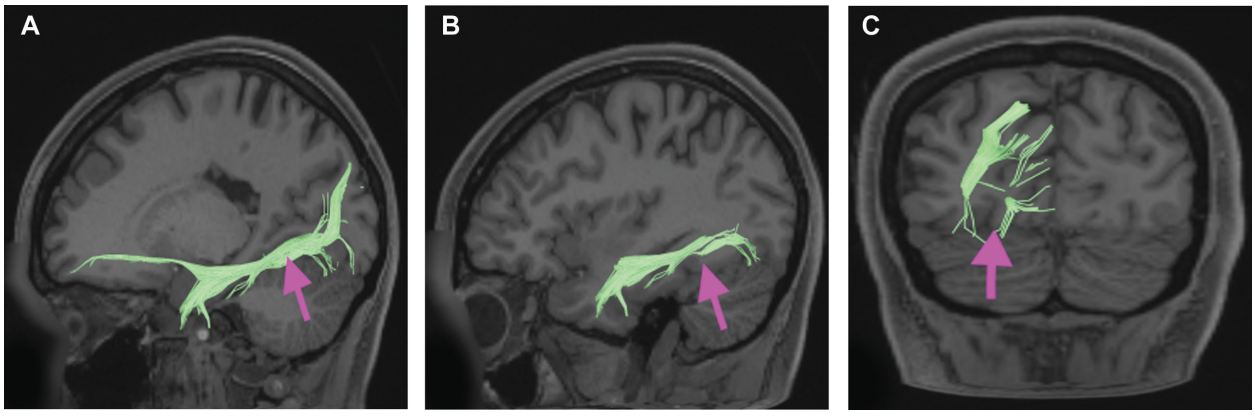

FIGURE 24. *Structural connectivity of VMV2 in the left hemisphere, shown on T1-weighted MR images. Sagittal views of* **A**, *medial and* **B**, *lateral planes, and* **C**, *coronal view. Light green: white matter tracts of VMV2 demonstrating connections with the ILF, IFOF, and VOF.*

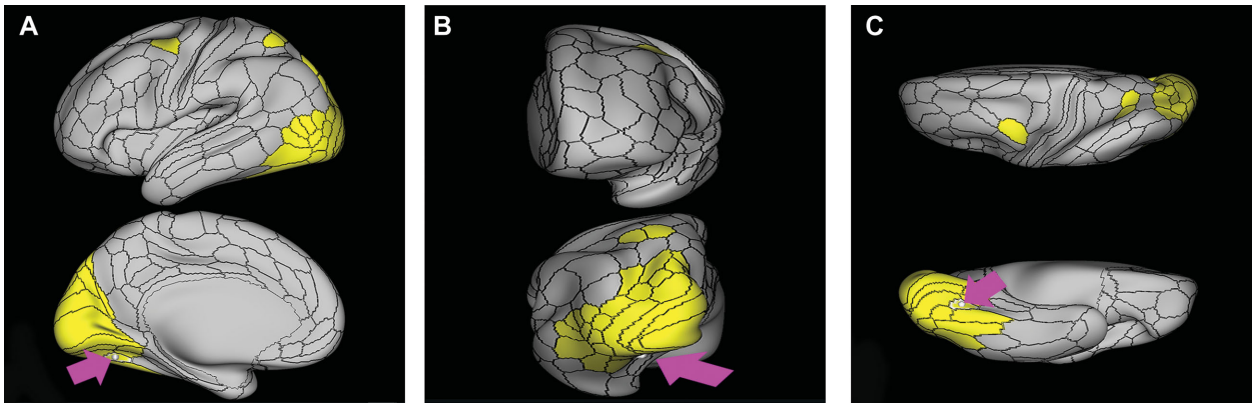

FIGURE 25. *Functional connectivity of VMV3 demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation of interest.*

Short association bundles are connected to V4, V3, VMV1, VMV2, PIT, V8, and PH (Figure 26).

What is known about its function? While area VMV3 is considered a new area, this region of the occipital lobe is suggested in the literature to be important for the integration of color, texture, and form information for higher level object recognition.[4,10]

Superior Surface Areas

The areas of the dorsal stream are aligned in a medial to lateral band between the early visual areas, the parieto-occipital sulcus and the posterior limit of the intraparietal sulcus. Thus, these areas start at the anterior precuneus and extend onto the lateral occipital surface just behind the intraparietral sulcus. The areas comprised by this region include V6, V6A, V7, V3a, and V3b (Figure 27). This area has consistent white matter connections with IFOF, MdLF, and the FM. V7 also connects with the ILF. The combined structural connectivity of these parcellations is shown in Figure 28.

Area V6

Where is it? Area V6 (visual area 6) is a vertically oriented area in the anterosuperior portion of the cuneus, just posterior to the superior parieto-occipital sulcus.

What are its borders? Area V6 borders the superior limbs of V2 and V3 posteriorly, and DVT anteriorly. V2 is its inferior boundary, and V6a is its superior boundary.

What is its functional connectivity? Area V6 demonstrates functional connectivity to areas 1, 2, 3a, 3b in the sensory strip,

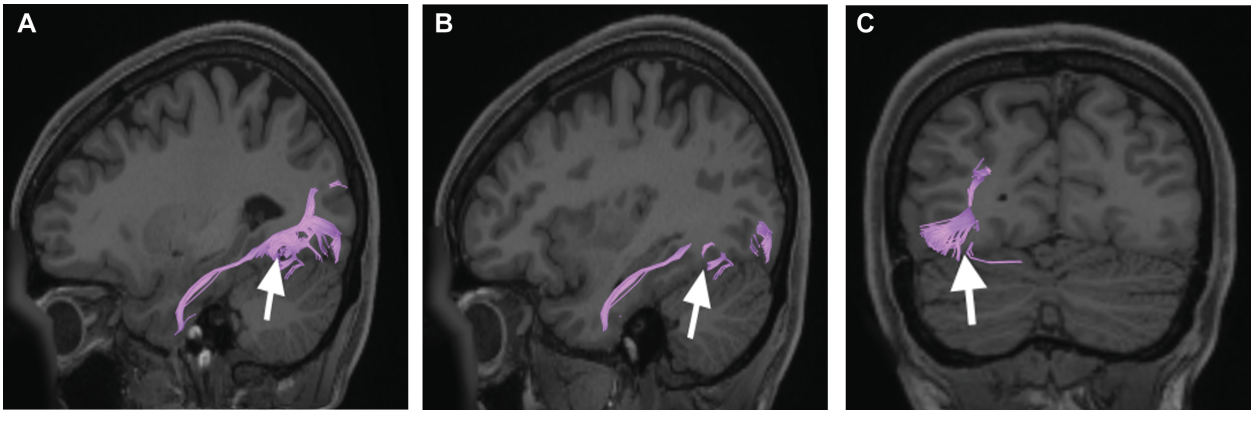

FIGURE 26. *Structural connectivity of VMV3 in the left hemisphere, shown on T1-weighted MR images. Sagittal views of* **A**, *medial and* **B**, *lateral planes, and* **C**, *coronal view. Purple: white matter tracts of VMV3 demonstrating connections with the ILF and VOF.*

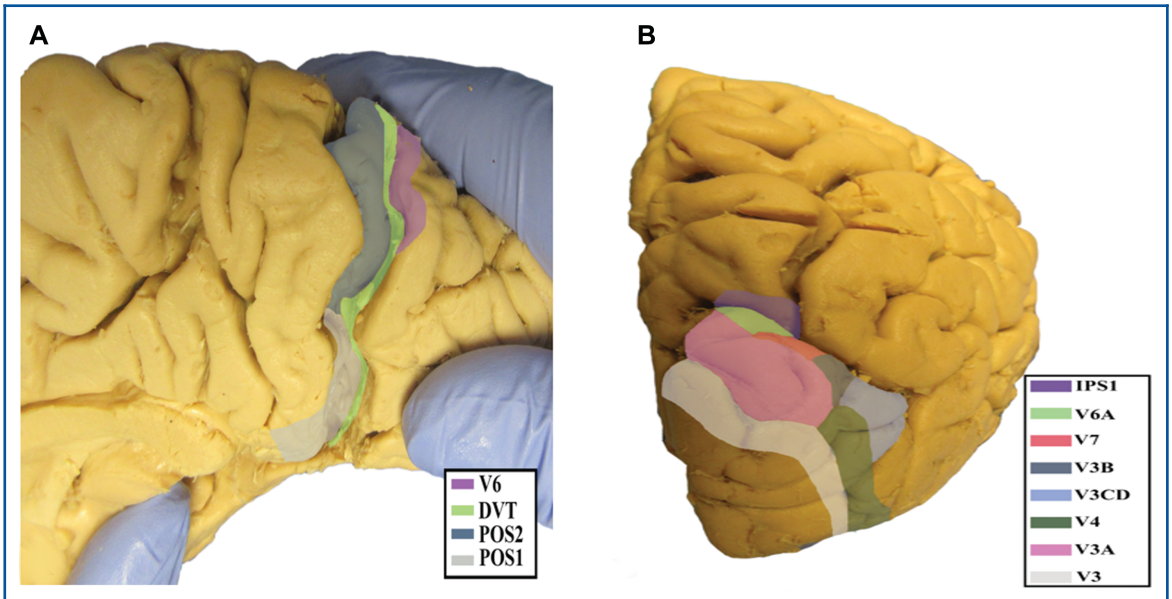

FIGURE 27. *Anatomic location of superior occipital lobe parcellations shown on the right hemisphere of a cadaver brain.* **A**, *Medial view of the occipital lobe with widening of the parietoccipital sulcus to show extension DVT and POS2.* **B**, *Posterior view of occipital lobe. Corresponding labels are shown in the lower right corner of each figure.*

area 4 in the motor strip, areas SCEF and FEF in the premotor region, areas 9-46d, and 46 in the lateral frontal lobe, areas a24prime, p32prime, 5mv, and 23c in the medial frontal lobe, areas FOP1, FOP3, FOP4, OP4, OP2-3, 43, PFcm, STV, PoI1, PoI2, MI, RI, TA2, 52, A4, MBelt, and PBelt in the insula opercular regions, areas 7PC, 7AL, 7am, VIP, LIPv, PGp, PFop, IPS1, IP0, PCV, and DVT in the parietal lobe, areas ProS, V1, V2, V3, and V4 in the medial occipital lobe, areas V3a, V3b, V7, and V6a of the dorsal visual stream, areas FFC, VVC, V8, VMV1, VMV2, and VMV3 of the ventral visual stream, and areas TPOJ2, TPOJ3, V3cd, V4t, LO1, LO2, LO3, MT, MST, PH, and FST of the lateral occipital lobe (Figure 29).

What are its white matter connections? Area V6 is structurally connected to the IFOF, MdLF, and FM. IFOF projections terminate at parcellelations in the frontal lobe including 9a, 9p, 9m, and 8BL. The MdLF runs parallel to the IFOF then courses laterally to the superior temporal gyrus, as the IFOF courses medially between the lateral ventricle and insula. The MdLF projections terminate at MBelt, A5, and PI. FM connections

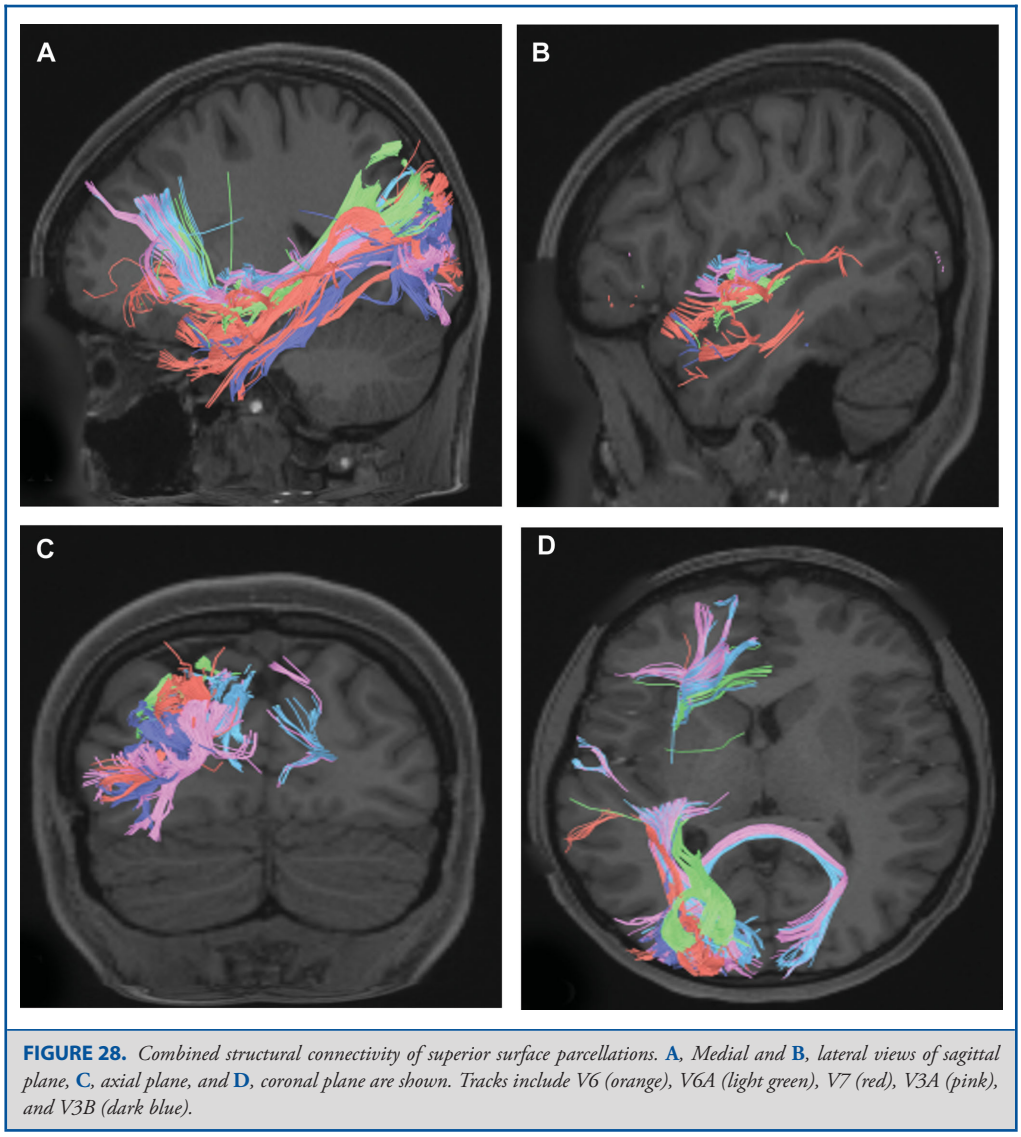

FIGURE 28. *Combined structural connectivity of superior surface parcellations.* **A**, *Medial and* **B**, *lateral views of sagittal plane,* **C**, *axial plane, and* **D**, *coronal plane are shown. Tracks include V6 (orange), V6A (light green), V7 (red), V3A (pink), and V3B (dark blue).*

travel through the splenium of the corpus callosum to terminate at V6, V2, and V1. Short association bundles are connected to V7, V3, V3b, and V3a. Right hemisphere has consistent ILF projections (Figure 30).

What is known about its function? Area V6 has been implicated in the processing and analysis of visual motion and has been demonstrated in lesion studies to cause motion blindness and other motion-related visual disturbances.[12]

Area V6A

Where is it? Area V6A (visual area 6a) is a small area that straddles the angle of the interhemispheric cleft of the superior occipital lobe, lying just posterior to the superior most limit of the parieto-occipital sulcus.

What are its borders? Area V6A borders V3a posteriorly, and DVT anteriorly. Its lateral border is made V7 and IPS1. V6 forms its inferior border.

What is its functional connectivity? Area V6A demonstrates functional connectivity to areas 1, 2, 3a, 3b in the sensory strip, area 4 in the motor strip, areas SCEF and FEF in the premotor region, areas a24prime, p32prime, 5mv, and 23c in the medial frontal lobe, areas OP4, 43, RI, A4, and PBelt in the insula opercular regions, areas 7PC, VIP, LIPv, PGp, IPS1, IP0, and DVT in the parietal lobe, areas ProS, V1, V2, V3, and V4 in the medial occipital lobe, areas V3a, V3b, V7, and V6 of the dorsal visual stream, areas FFC, VVC, V8, VMV1, VMV2, and VMV3 of the ventral visual stream, and areas TPOJ2, V3cd, V4t, LO1,

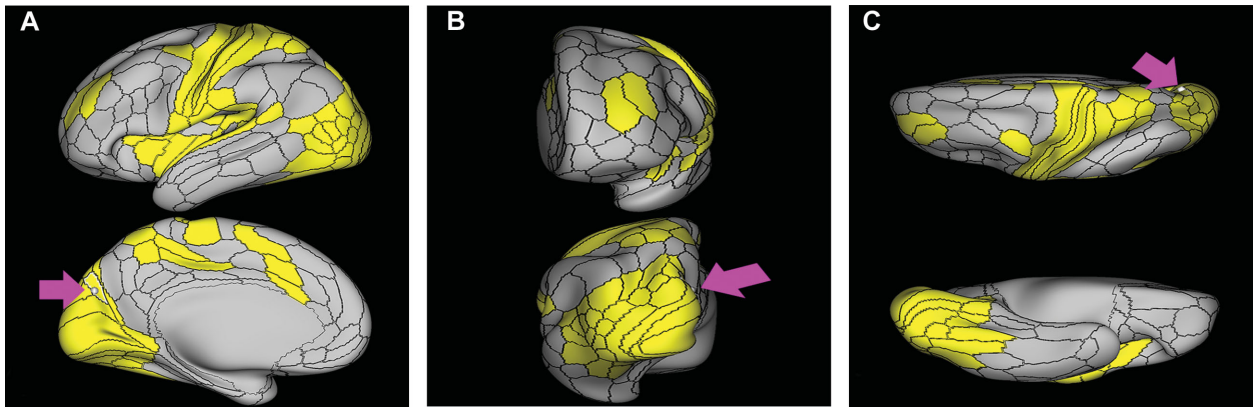

FIGURE 29. *Functional connectivity of V6 demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation of interest.*

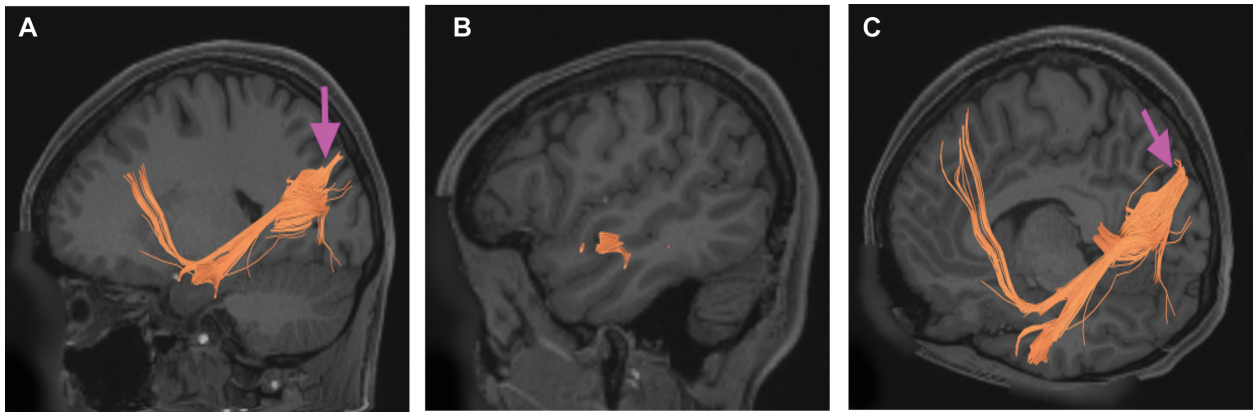

FIGURE 30. *Structural connectivity of V6 in the left hemisphere, shown on T1-weighted MR images. Sagittal views of* **A**, *medial and* **B**, *lateral planes, and* **C**, *oblique view. Orange: white matter tracts of V6 demonstrating connections with the IFOF, MdLF, and FM.*

LO2, LO3, MT, MST, PH, and FST of the lateral occipital lobe (Figure 31).

What are its white matter connections? Area V6A is structurally connected to the IFOF and MdLF. There are inconsistent projections with FM. IFOF projections terminate at frontal lobe parcellations 8BM and 8BL. The MdLF fibers run parallel to the IFOF then course laterally to the superior temporal gyrus to terminate at A4 and MBelt. Short association bundles are connected to V3B and V7 (Figure 32).

What is known about its function? Area V6A responds to peripheral visual stimuli and has been implicated in the integration and evaluation of spatial information to coordinate eye and arm movements, indicating its importance for reaching and hand–eye coordination.[13]

Area V7

Where is it? Area V7 (visual area 7) is found on the superior surface of the occipital lobe near the interhemispheric cleft, roughly lateral to the superior most point of the intraparietal sulcus.

What are its borders? Area V7 borders V3a posteriorly, and IPS1 anteriorly. Its lateral border is made up of V3b, and its medial border is formed by V6a.

What is its functional connectivity? Area V7 demonstrates functional connectivity to areas 1, 2, 3a, 3b in the sensory strip, area 4 in the motor strip, areas SCEF and FEF in the premotor region, areas a24prime, p32prime, and 23c in the medial frontal lobe, areas OP4, 43, MI, RI, A4, LBelt, and PBelt in the insula opercular regions, areas VIP, LIPv, IPS1, IP0, and DVT in the

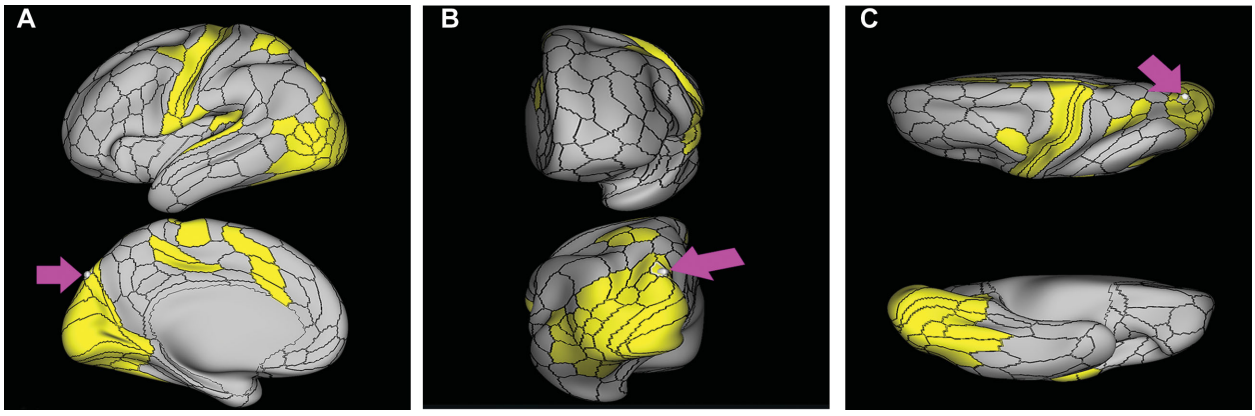

FIGURE 31. *Functional connectivity of V6A demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation of interest.*

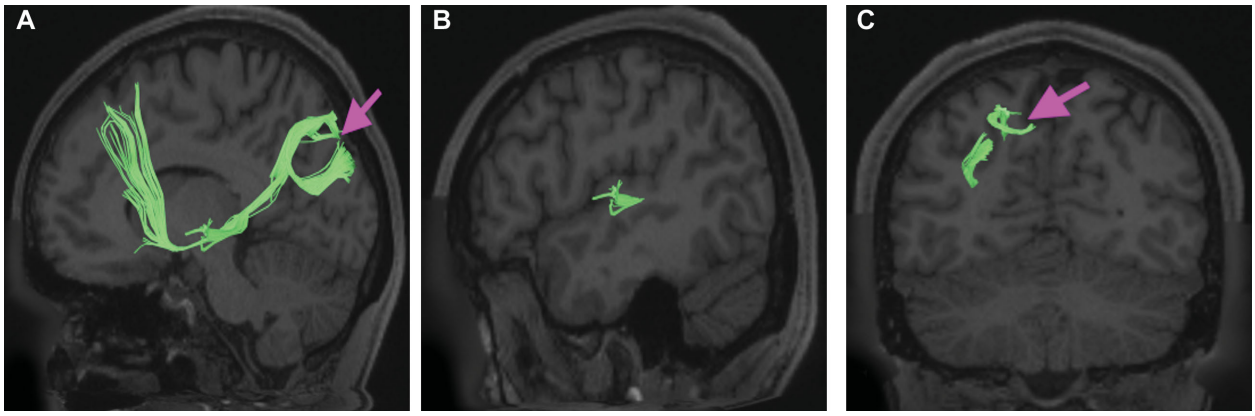

FIGURE 32. *Structural connectivity of V6A in the left hemisphere, shown on T1-weighted MR images. Sagittal views of* **A**, *medial and* **B**, *lateral planes, and* **C**, *coronal view. Light green: white matter tracts of V6A demonstrating connections with the IFOF and MdLF.*

parietal lobe, areas ProS, V1, V2, V3, and V4 in the medial occipital lobe, areas V3a, V3b, V6, and V6a of the dorsal visual stream, areas FFC, VVC, V8, VMV1, VMV2, and VMV3 of the ventral visual stream, and areas V3cd, V4t, LO1, LO2, LO3, MT, MST, PH, and FST of the lateral occipital lobe (Figure 33).

What are its white matter connections? Area V7 is structurally connected with IFOF, MdLF, and ILF. The termination of the IFOF is inconsistent across brains. The MdLF fibers run parallel to the IFOF then course laterally to the superior temporal gyrus to terminate at A5, STSda, STSdp, STSva, and TGd. ILF projections travel through the temporal lobe to end at TGv and TGd. Short association bundles are connected to LO1, LO2, LO3, V3CD, V3A, V6A, and V6 (Figure 34).

What is known about its function? Area V7 contains a relatively narrow retinotopic map of the central visual field surrounding the foveal point and shows increased stimulation in response to attention directed toward a visual stimulus.[1] Area V7 uses this visual information to integrate spatial information within the central visual field.[14]

Area V3a

Where is it? Area V3a (visual area 3a) is found in the superior surface of the occipital lobe, near the interhemispheric fissure. It is positioned similar to the superior limb of V4, which as described above, is hypoplastic compared to V3.

What are its borders? Area V3a borders V3 inferiorly, and V4 posteriorly. Its lateral border is V3b. Its anterior border included

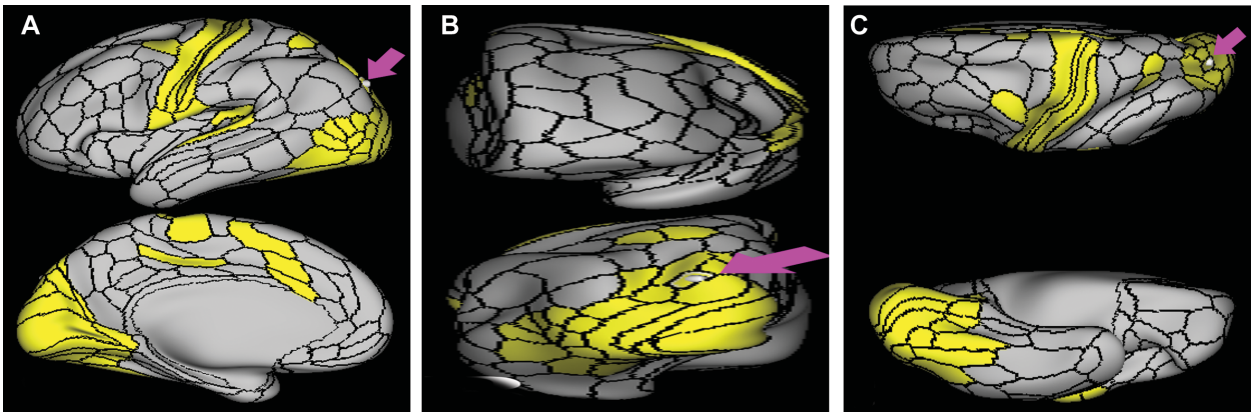

FIGURE 33. *Functional connectivity of V7 demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation of interest.*

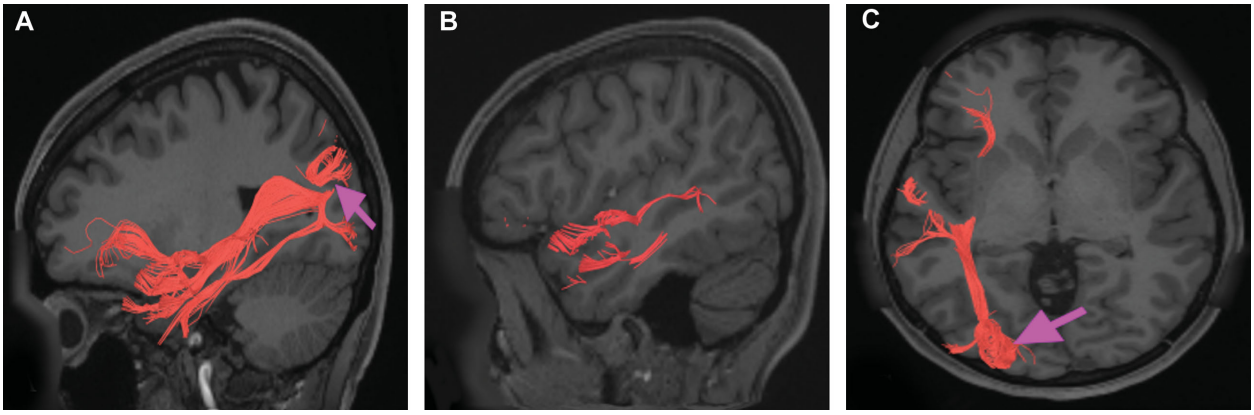

FIGURE 34. *Structural connectivity of V7 in the left hemisphere, shown on T1-weighted MR images. Sagittal views of* **A**, *medial and* **B**, *lateral planes, and* **C**, *axial view. Red: white matter tracts of V7 demonstrating connections with the IFOF, MdLF, and ILF.*

V7 and V6a. V6 is its anterior neighbor across the interhemispheric cleft.

What is its functional connectivity? Area V3a demonstrates functional connectivity to areas 1, 3a, 3b in the sensory strip, area 4 in the motor strip, areas SCEF and FEF in the premotor region, areas a24prime, p32prime, 5mv, and 23c in the medial frontal lobe, areas FOP1, FOP3, FOP4, OP4, OP2-3, 43, PFcm, PoI1, RI, 52, A4, LBelt, and PBelt in the insula opercular regions, areas VIP, LIPv, PGp, PFop, IPS1, IP0, and DVT in the parietal lobe, areas ProS, V1, V2, V3, and V4 in the medial occipital lobe, areas V3b, V7, V6, and V6a of the dorsal visual stream, areas FFC, VVC, V8, VMV1, VMV2, and VMV3 of the ventral visual stream, and areas TPOJ2, V3cd, V4t, LO1, LO2, LO3, MT, MST, PH, and FST of the lateral occipital lobe (Figure 35).

What are its white matter connections? Area V3a is structurally connected to the IFOF, MdLF, and FM. The IFOF has consistent terminations to the frontal lobe at parcellations 8BL, 9a, 9p, 9m, 10pp, and 10d. There are projections from the MdLF to the superior temporal gyrus that terminate at STGa. FM connections course through the splenium of the corpus callosum to terminate at contralateral V3a. V3a has short association bundles connected to V6A, V3b, V6, V7, and V3. Right hemisphere has inconsistent projections with the IFOF when compared to left hemisphere (Figure 36).

What is known about its function? Area V3a demonstrates high motion sensitivity and high contrast sensitivity in the central visual field surrounding the foveal point indicating its role in motion-selective visual perception.[15] This region also integrates

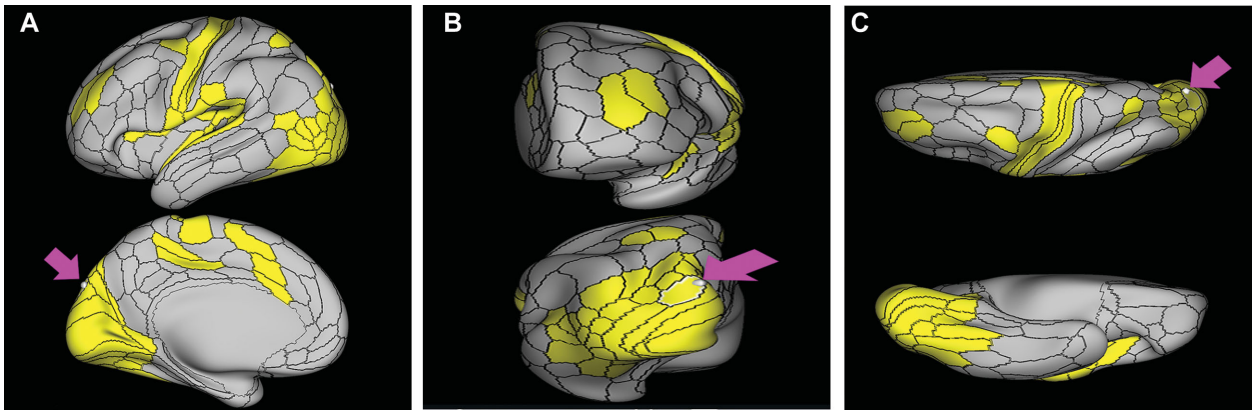

FIGURE 35. *Functional connectivity of V3A demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation of interest.*

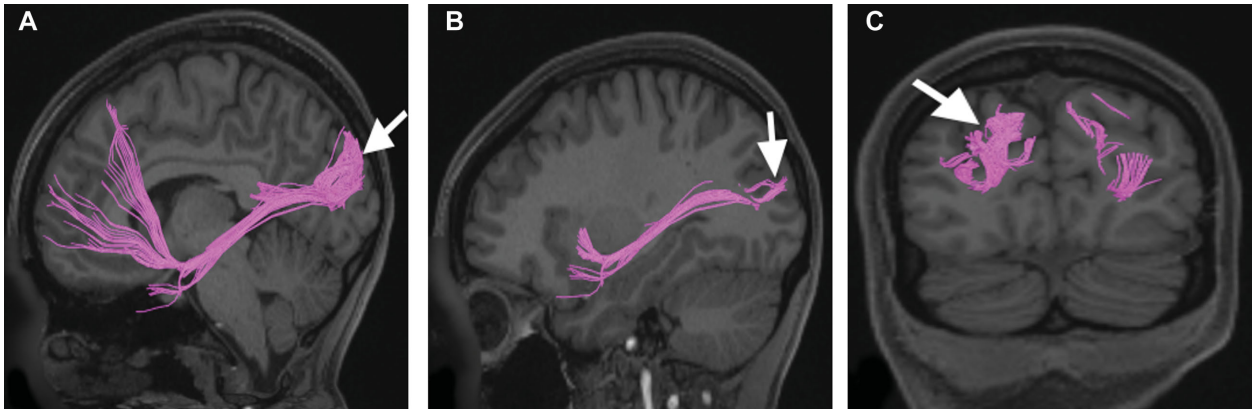

FIGURE 36. *Structural connectivity of V3A in the left hemisphere, shown on T1-weighted MR images. Sagittal views of* **A**, *medial and* **B**, *lateral planes, and* **C**, *coronal view. Pink: white matter tracts of V3A demonstrating connections with the IFOF, MdLF, and FM.*

spatial information from contralateral and ipsilateral visual input sources.[16]

Area V3b

Where is it? Area V3b (visual area 3b) is found on the superior occipital surface.

What are its borders? Area V3b borders IP0 anterolaterally, IPS1 anteromedially, and V7 medially. Its posterior border is made up of V3a and the superior limb of V4. V3cd is its lateral neighbor.

What is its functional connectivity? Area V3b is connected to areas SCEF and FEF in the premotor region, areas a24prime, p32prime, and 23c in the medial frontal lobe, areas 43, RI, and PBelt in the insula opercular regions, areas 7PC, VIP, IPS1, IP0, and DVT in the parietal lobe, areas ProS, V1, V2, V3, and V4 in the medial occipital lobe, areas V3a, V7, V6, and V6a of the dorsal visual stream, areas FFC, VVC, V8, VMV1, VMV2, and VMV3 of the ventral visual stream, and areas V3cd, V4t, LO1, LO2, LO3, MT, MST, PH, and FST of the lateral occipital lobe (Figure 37).

What are its white matter connections? Area V3b is structurally connected with local parcellations. There are connections with IFOF and MdLF but this is inconsistent across brains. Short association bundles are connected to MIP, IPO, IPS1, V4, and V3CD (Figure 38).

What is known about its function? Area V3b acts as a relay point, collecting motion-sensitive information from the dorsal stream, and is implicated in the processing of motion information and

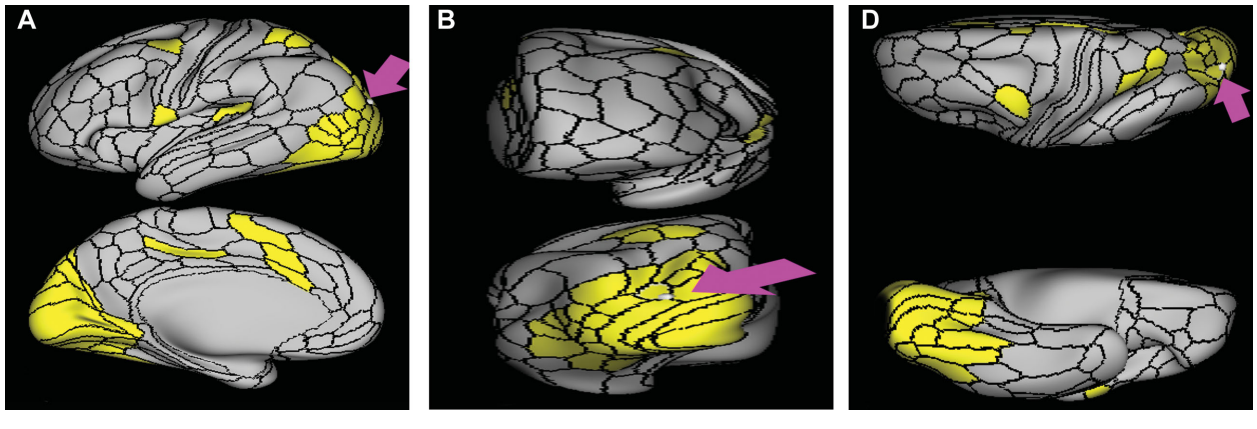

FIGURE 37. *Functional connectivity of V3B demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation of interest.*

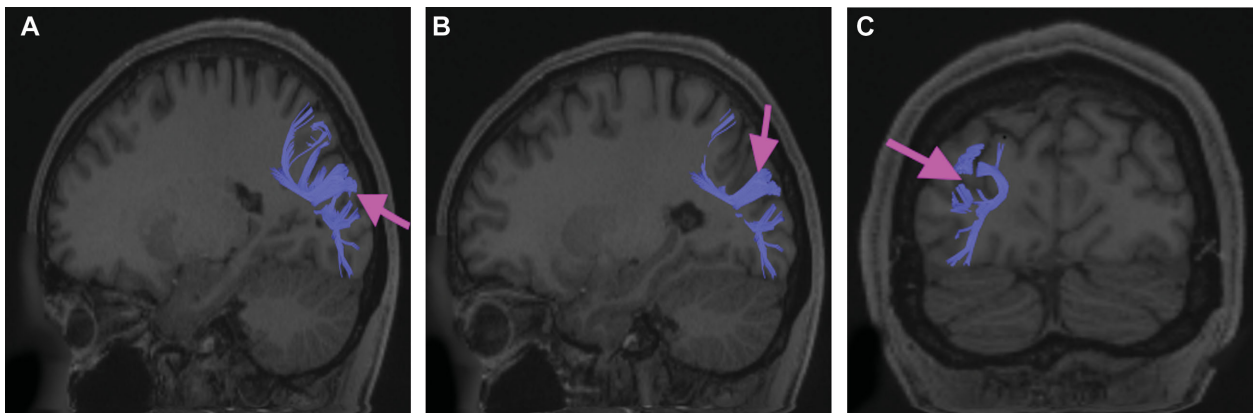

FIGURE 38. *Structural connectivity of V3B in the left hemisphere, shown on T1-weighted MR images. Sagittal views of* **A**, *medial and* **B**, *lateral planes, and* **C**, *coronal view showing. Dark blue: white matter tracts of V3B demonstrating connections with local parcellations.*

discerning the edges of moving objects, known as kinetic boundaries.[10]

Lateral Surface Areas

Though numerous, these small areas are clustered on the small triangle of the lateral occipital lobe bounded by the posterior portions of MTG anteriorly, the angular gyrus superiorly, and the tentorium inferiorly. Given the notorious lack of repetitive patterns in the lateral occipital sulcus, accurate localization is difficult. The areas comprised of this region include V3cd, LO1, LO2, LO3, V4t, MT, MST, FST, and PH (Figure 39). This area has consistent white matter connections with ILF. Areas FST and PH also connect with the SLF. The combined tractography of these parcellations is shown in Figure 40.

Area V3cd

Where is it? Area V3cd (visual area 3 c/d) is a vertical strip in the posterosuperior portion of the lateral occipital lobe, just posterior to the angular gyrus.

What are its borders? Area V3cd borders PGp and LO3 anteriorly, LO1 inferiorly, V4 posteriorly, and V3b superiorly.

What is its functional connectivity? Area V3cd demonstrates functional connectivity to area FEF in the premotor region, area PBelt in the insula and opercular region, areas 7PC, AIP, VIP, LIPv, PGp, IPS1, IP0, and DVT in the parietal lobe, areas ProS, V1, V2, V3, and V4 in the medial occipital lobe, areas V3a, V3b, V7, V6, and V6a of the dorsal visual stream, areas VVC, V8, VMV1, VMV2, and VMV3 of the ventral visual stream, and areas

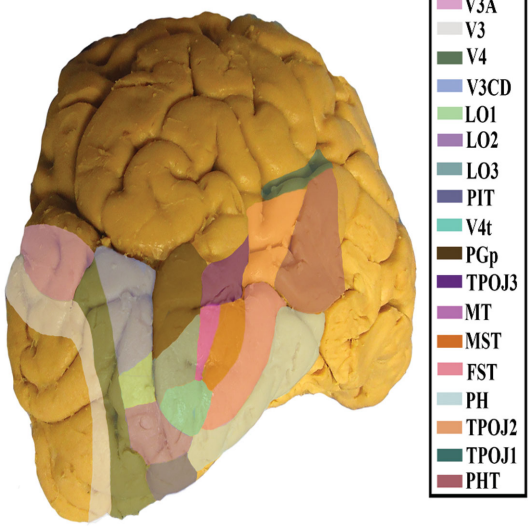

FIGURE 39. *Anatomic location of lateral occipital lobe parcellations shown on the right hemisphere of a cadaver brain. Oblique lateral view of the occipital lobe. Corresponding labels are shown in the lower right corner of each figure.*

V3cd, MT, MST, V4t, LO1, LO2, LO3, PH, and FST of the lateral occipital lobe (Figure 41).

What are its white matter connections? Area V3cd is structurally connected to local parcellations. Short association bundles are connected to V3B, V7, V4t, V3CD, LO1, LO2, LO3, MST, and MT (Figure 42).

What is known about its function? Area V3cd integrates object detail information, such as contrast and kinetic edges,[10,15] to create an holistic image for object recognition.[11]

Area LO1

Where is it? Area LO1 is a small vertically oriented area in the posterior occipital lobe, just anterior to the occipital pole.

What are its borders? Area LO1 borders V4 posteriorly, and LO3 anteriorly. Its superior border is made up of V3cd. V4t and LO2 form its inferior border.

What is its functional connectivity? Area LO1 demonstrates functional connectivity to area FEF in the premotor region, area A4 in the insula and opercular region, areas VIP, LIPv, IP0, DVT, and IPS1 in the parietal lobe, areas V1, V2, V3, and V4 in the medial occipital lobe, areas V3a, V3b, V7, V6, and V6a of the dorsal visual stream, areas FFC, VVC, V8, PIT, VMV1, VMV2, and VMV3 of the ventral visual stream, and areas V3cd, V4t, MT, LO2, LO3, PH, and FST of the lateral occipital lobe (Figure 43).

What are its white matter connections? Area LO1 is structurally connected to local parcellations. Short association bundles are connected to V3A, V3B, V3CD, LO2, and LO3 (Figure 44).

What is known about its function? Area LO1 is a higher order visual structure that receives detail, motion, and characteristic information about the central visual field from both the dorsal and ventral streams. Area LO1 preferentially activates in response to orientation-selective and boundary information to process the form of objects.[5,11,17]

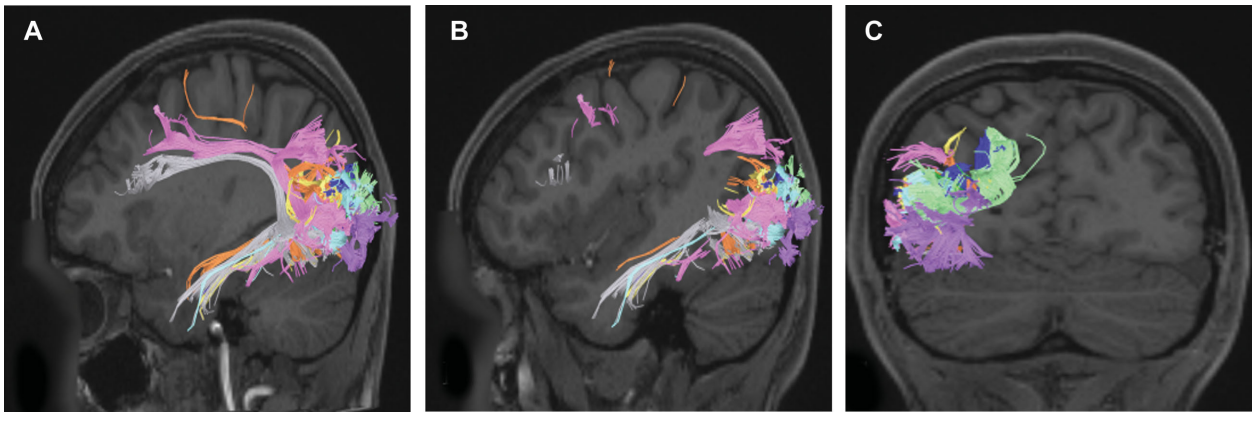

FIGURE 40. *Combined structural connectivity of lateral surface parcellations.* **A**, *Medial and* **B**, *lateral views of sagittal plane, and* **C**, *coronal plane are shown. Tracks include V3cd (light blue), LO1 (light green), LO2 (purple), LO3 (turquoise), V4t (green), MT (yellow), MST (orange), FST (pink), and PH (gray).*

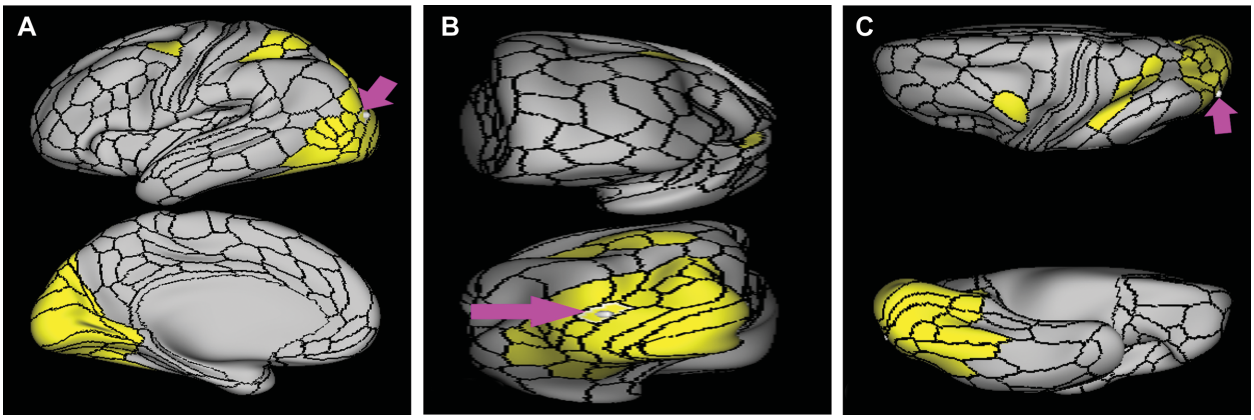

FIGURE 41. *Functional connectivity of V3cd demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation of interest.*

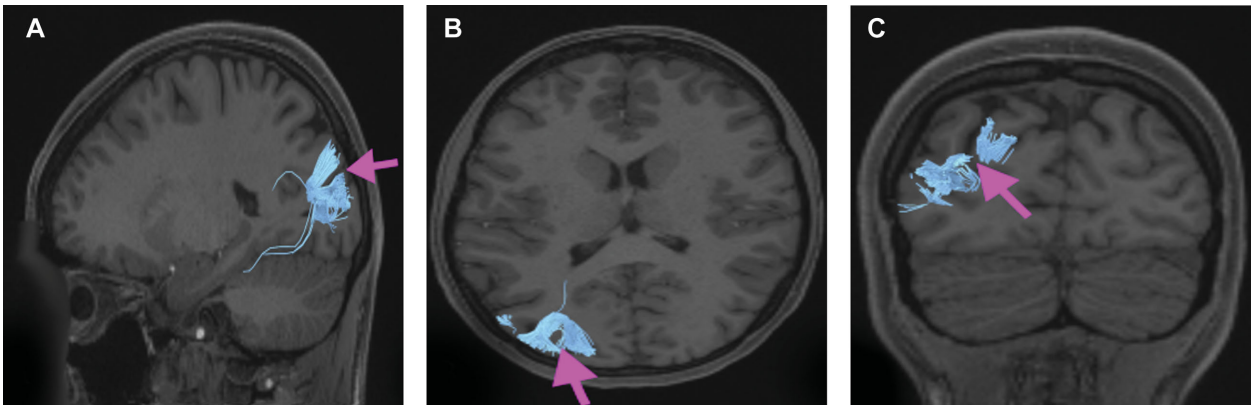

FIGURE 42. *Structural connectivity of V3cd in the left hemisphere, shown on T1-weighted MR images.* **A**, *Sagittal,* **B**, *axial, and* **C**, *coronal planes. Light blue: white matter tracts of V3cd demonstrating connections with local parcellations.*

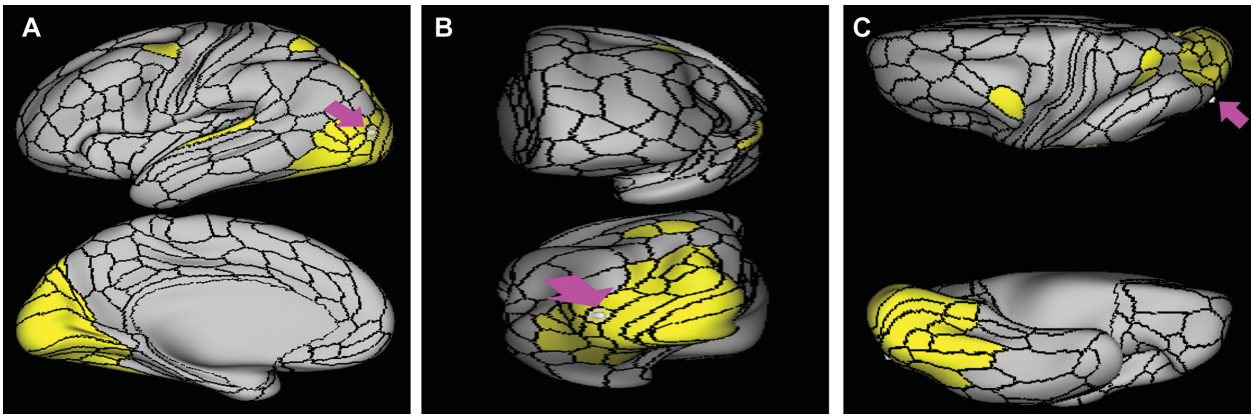

FIGURE 43. *Functional connectivity of LO1 demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation of interest.*

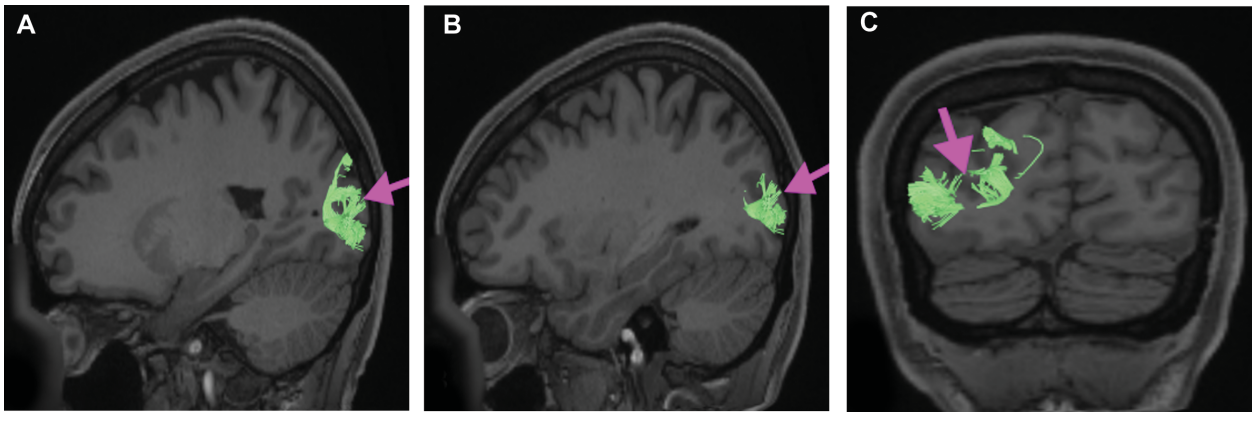

FIGURE 44. *Structural connectivity of LO1 in the left hemisphere, shown on T1-weighted MR images. Sagittal views of* **A**, *medial and* **B**, *lateral planes, and* **C**, *coronal view. Light green: white matter tracts of LO1 demonstrating connections with local parcellations.*

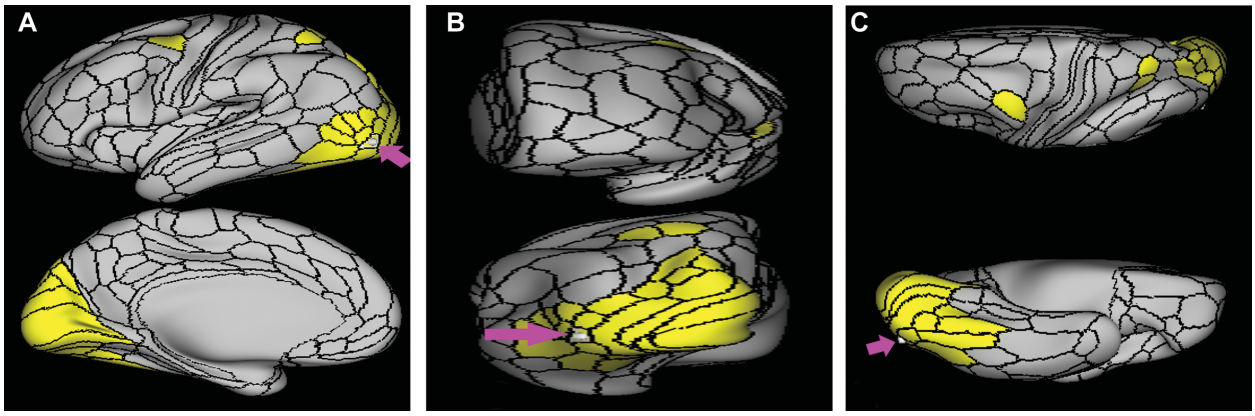

FIGURE 45. *Functional connectivity of LO2 demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation of interest.*

Area LO2

Where is it? Area LO2 is a small horizontally oriented area just anterior to the occipital pole and slightly superior to the tentorium.

What are its borders? Area LO2 borders V4 posteriorly, and PH anteriorly. Its superior border is V4t and its inferior border is PIT.

What is its functional connectivity? Area LO2 demonstrates functional connectivity to area FEF in the premotor region, area PBelt in the insula and opercular region, areas VIP, LIPv, and IPS1 in the parietal lobe, areas V1, V2, V3, and V4 in the medial occipital lobe, areas V3a, V3b, V7, V6, and V6a of the dorsal visual stream, areas FFC, VVC, V8, PIT, and VMV3 of the ventral visual stream, and areas V3cd, V4t, MT, LO1, LO3, PH, and FST of the lateral occipital lobe (Figure 45).

What are its white matter connections? Area LO2 is structurally connected to local parcellations. Short association bundles are connected to V3A, V3B, V3CD, LO1, and LO3 (Figure 46).

What is known about its function? Area LO2 shows preferential retinotopic activation in the peripheral visual field, and integrates inputs from the ventral and dorsal streams to encode information about the shapes of stimuli. This region also demonstrates high activation in the processing, encoding, and recognition of objects.[5,11,17]

Area LO3

Where is it? Area LO3 is a vertically oriented area in the superior central portion of the lateral occipital lobe. It is located just inferior to the posterior angular gyrus.

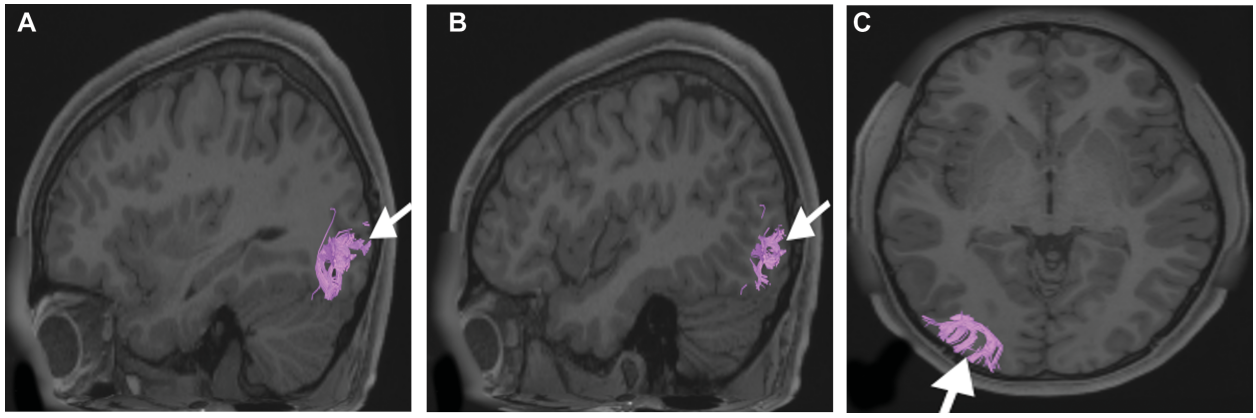

FIGURE 46. *Structural connectivity of LO2 in the left hemisphere, shown on T1-weighted MR images. Sagittal views of* **A**, *medial and* **B**, *lateral planes, and* **C**, *axial view. Purple: white matter tracts of LO2 demonstrating connections with local parcellations.*

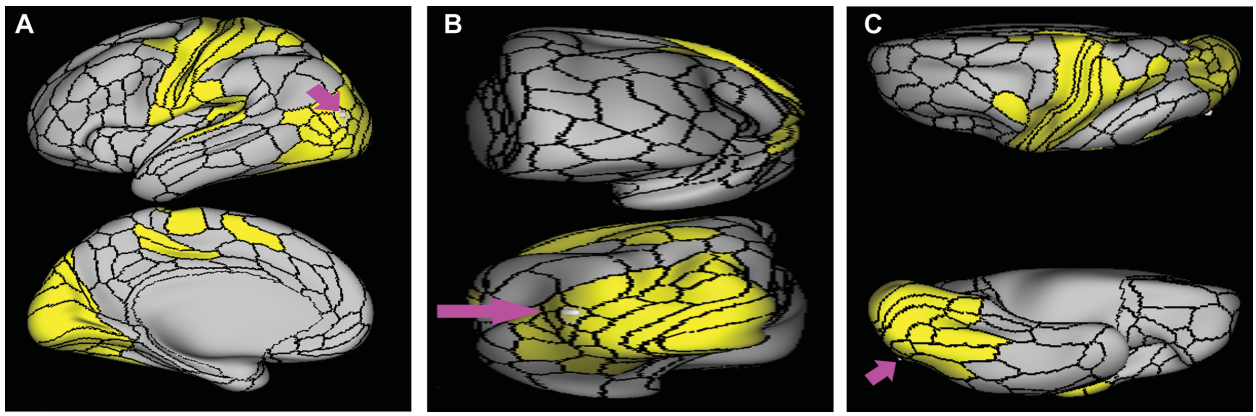

FIGURE 47. *Functional connectivity of LO3 demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation of interest.*

What are its borders? Area LO3 borders V3cd and LO1 posteriorly, and MT anteriorly. Its superior border is made up of TPOJ3 and PGp. Its inferior border is made up of LO1 and V4t.

What is its functional connectivity? Area LO3 demonstrates functional connectivity to areas 1,2, 3a, and 3b in the sensory strip, area 4 in the motor strip, areas SCEF and FEF in the premotor region, areas 5mv and 23c in the cingulate regions, areas OP4, PFcm, 43, RI, PBelt, and A4 in the insula and opercular region, areas 7PC, DVT, PFop, PGp, VIP, LIPv, IP0, and IPS1 in the parietal lobe, areas V1, V2, V3, and V4 in the medial occipital lobe, areas V3a, V3b, V7, V6, and V6a of the dorsal visual stream, areas FFC, VVC, V8, PIT, VMV1, VMV2, and VMV3 of the ventral visual stream, and areas TPOJ2, TPOJ3 V3cd, V4t, MT, LO1, LO2, PH, and FST of the lateral occipital lobe (Figure 47).

What are its white matter connections? Area LO3 is structurally connected to the ILF and local parcellations. ILF projections travel through the temporal lobe to terminate at TGv. Short association bundles are connected to V3A, V3B, V3CD, LO1, LO2, PH, and FST (Figure 48).

What is known about its function? While LO3 is considered a new area, the literature suggests this region of the occipital lobe is an important hub between the dorsal and ventral streams to integrate, encode, and process detail, motion, and shape information for object recognition and encoding.[5,11]

Area V4t

Where is it? Area V4t (visual area 4t) is a horizontal area in the central portion of the lateral occipital cortex.

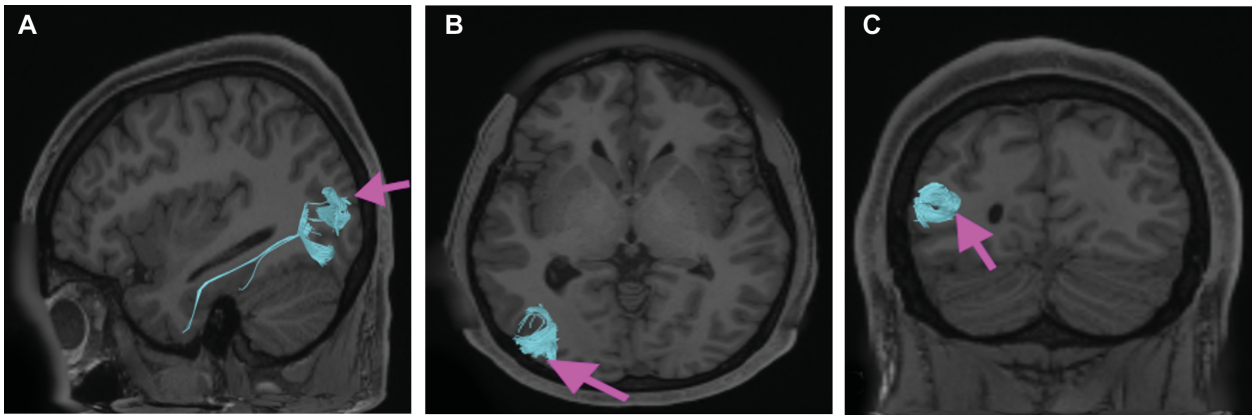

FIGURE 48. *Structural connectivity of LO3 in the left hemisphere, shown on T1-weighted MR images.* **A**, *Sagittal,* **B**, *axial, and* **C**, *coronal planes. Turquoise: white matter tracts of LO3 demonstrating connections with ILF and local parcellations.*

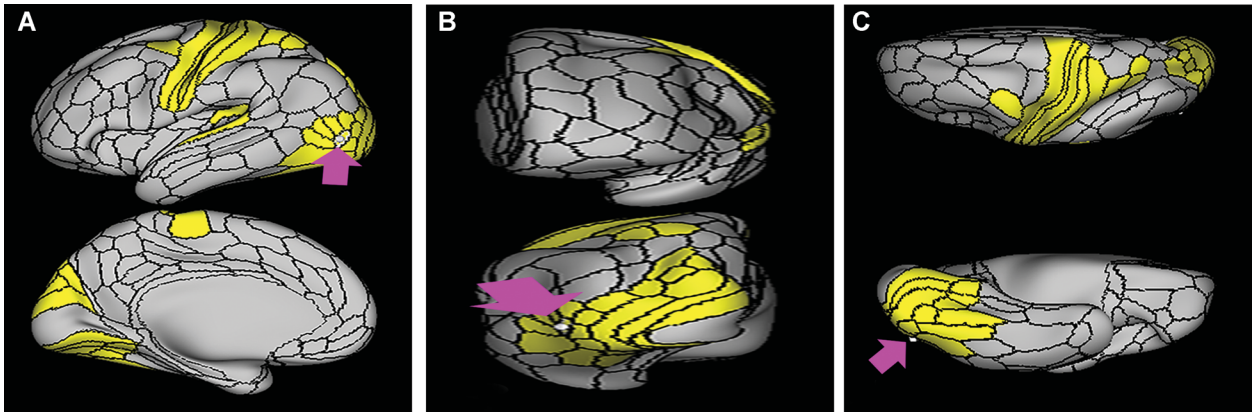

FIGURE 49. *Functional connectivity of V4t demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation of interest.*

What are its borders? Area V4t borders LO1 posteriorly, and FST anteriorly. Its inferior border is LO2. Its superior border is made up of MT, MST, and LO3.

What is its functional connectivity? Area V4t demonstrates functional connectivity to areas 1, 2, 3a, and 3b in the sensory strip, area 4 in the motor strip, area FEF in the premotor region, areas RI, PBelt, and A4 in the insula and opercular region, areas VIP, LIPv, and IPS1 in the parietal lobe, areas V2, V3, and V4 in the medial occipital lobe, areas V3a, V3b, V7, V6, and V6a of the dorsal visual stream, areas VVC, V8, VMV1, VMV2, and VMV3 of the ventral visual stream, and areas V3cd, MT, MST, LO3, PH, and FST of the lateral occipital lobe (Figure 49).

What are its white matter connections? Area V4t is structurally connected with local parcellations. Tracts originating from this region such as SLF and ILF are inconsistent across brains. Short association bundles are connected to V4t, LO3, MST, MT, LO1, and V3CD (Figure 50).

What is known about its function? Area V4t has been shown in the literature to integrate information from both the ventral and dorsal streams, and demonstrates a high level of activity in response to both motion and shape-sensitive information, indicating its significance in the integration of object processing and global-motion perception.[18]

Area MT

Where is it? Area MT is a vertically oriented area in the superior part of the central lateral occipital lobe. It is located just inferior to the angular gyrus.

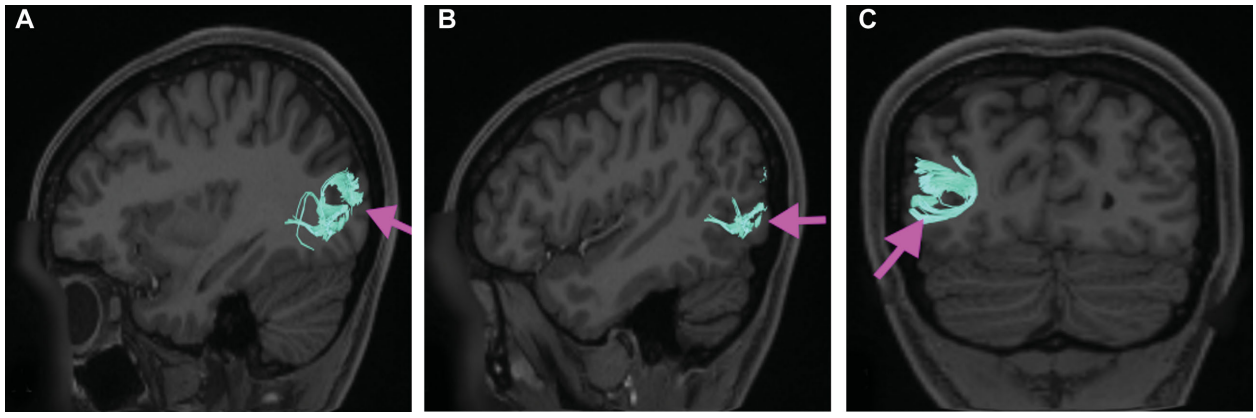

FIGURE 50. *Structural connectivity of V4t in the left hemisphere, shown on T1-weighted MR images. Sagittal views of* **A**, *medial and* **B**, *lateral planes, and* **C**, *coronal view. Green: white matter tracts of V4t demonstrating connections with local parcellations.*

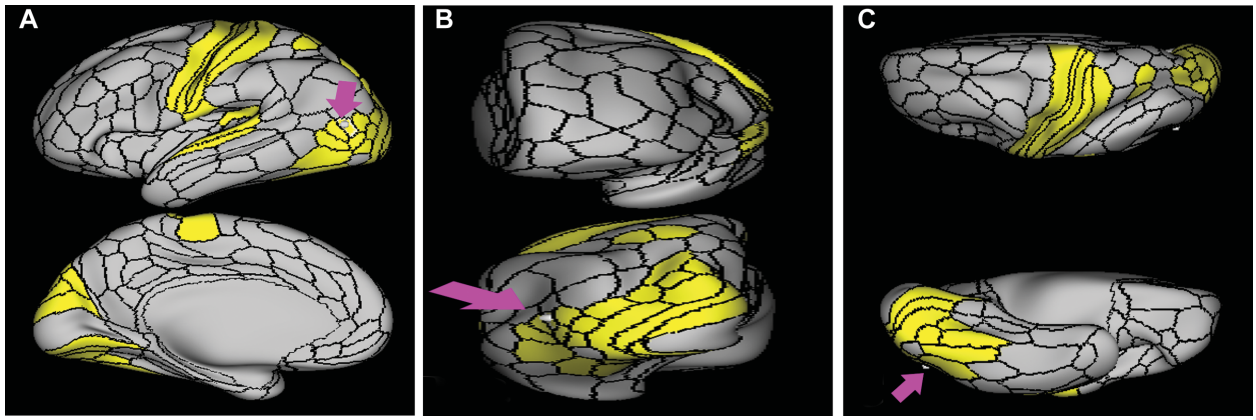

FIGURE 51. *Functional connectivity of MT demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation of interest.*

What are its borders? Area MT borders LO3 posteriorly, and MST anteriorly. Its superior border is formed by TPOJ3 and its inferior border by V4t.

What is its functional connectivity? Area MT demonstrates functional connectivity to areas 1, 2, 3a, and 3b in the sensory strip, area 4 in the motor strip, areas OP4, RI, PBelt, A4, and A5 in the insula and opercular region, areas VIP, LIPv, and IPS1 in the parietal lobe, areas V2, V3, and V4 in the medial occipital lobe, areas V3a, V3b, V7, V6, and V6a of the dorsal visual stream, areas FFC, VVC, V8, PIT, VMV3 of the ventral visual stream, and areas V3cd, V4t, MST, LO1, LO2, LO3, PH, and FST of the lateral occipital lobe (Figure 51).

What are its white matter connections? Area MT is structurally connected with the ILF. These projections are inconsistent across brains. ILF projections travel through the temporal lobe to end at TF. There are many short association bundles connecting to MST, LO1, LO2, LO3, TPOJ2, TPOJ3, FST, PH, V3b, and IPO (Figure 52).

What is known about its function? Neurons in area MT respond to direction-sensitive visual motion and are responsible for the integration of one-dimensional visual signals into a two-dimensional visual motion pattern, binocular disparity tuning, noise reduction, segmentation of figure and background in complex and moving stimuli, and initiation of smooth-pursuit eye movements.[19,20]

Area MST

Where is it? Area MST is a vertically oriented area found paralleling and just anterior to MT, just below the angular gyrus.

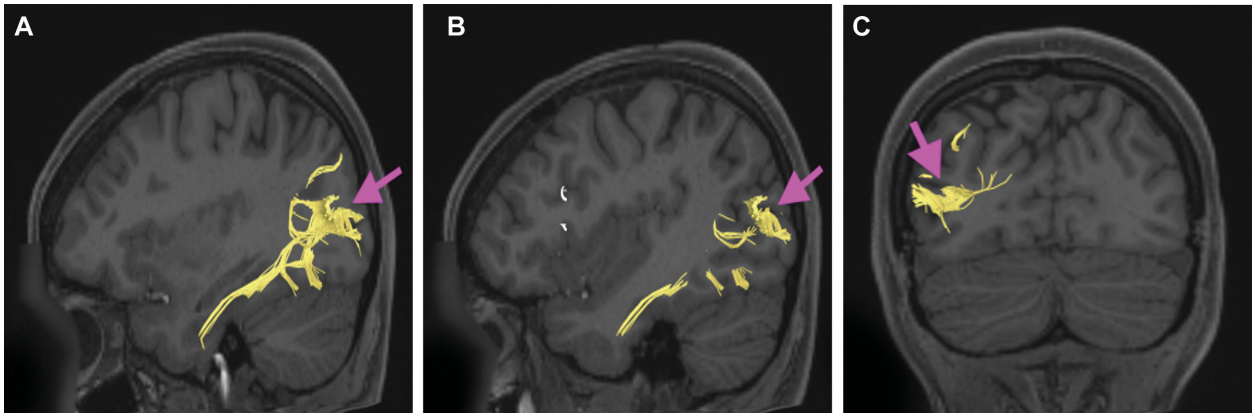

FIGURE 52. *Structural connectivity of MT in the left hemisphere, shown on T1-weighted MR images. Sagittal views of* **A**, *medial and* **B**, *lateral planes, and* **C**, *coronal view. Yellow: white matter tracts of MT demonstrating connections with ILF.*

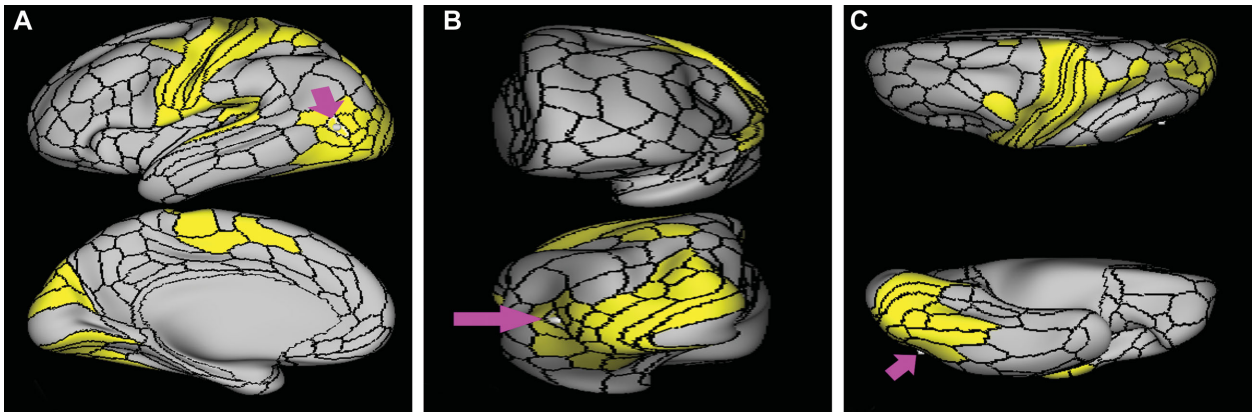

FIGURE 53. *Functional connectivity of MST demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation of interest.*

What are its borders? Area MST borders MT posteriorly, and FST anteriorly. Its superior border is made up of TPOJ2 and TPOJ3. Its inferior border is formed by FST and V4t.

What is its functional connectivity? Area MST demonstrates functional connectivity to areas 1, 2, 3a, and 3b in the sensory strip, area 4 in the motor strip, areas SCEF, FEF, and 6v in the premotor region, area 24dd in the cingulate regions, areas OP1, OP4, PFcm, 43, RI, LBelt, PBelt, and A4 in the insula and opercular region, areas 7PC, VIP, LIPv, and IPS1 in the parietal lobe, areas V2, V3, and V4 in the medial occipital lobe, areas V3a, V3b, V7, V6, and V6a of the dorsal visual stream, areas FFC, VVC, V8, PIT, VMV3 of the ventral visual stream, and areas TPOJ2, V3cd, V4t, MT, LO1, LO2, LO3, PH, and FST of the lateral occipital lobe (Figure 53).

What are its white matter connections? Area MST is structurally connected to the ILF. This parcellation also has inconsistent SLF connections. ILF projections travel through the temporal lobe to terminate at TGv. Short association bundles are connected to MT, PH, TE2p, and FST (Figure 54).

What is known about its function? Area MST receives direct, functional input from area MT and is responsible for the integration and analysis of global, visual motion and the perception of self-motion.[21] It is also involved in the execution and continuation of smooth pursuit eye movements, in coordination with the frontal eye fields.[19,20]

Area FST

Where is it? Area FST is found is an oblique to slightly vertically oriented area in the anterior portion of the lateral occipital lobe. It is just posterior to the end of the MT gyrus.

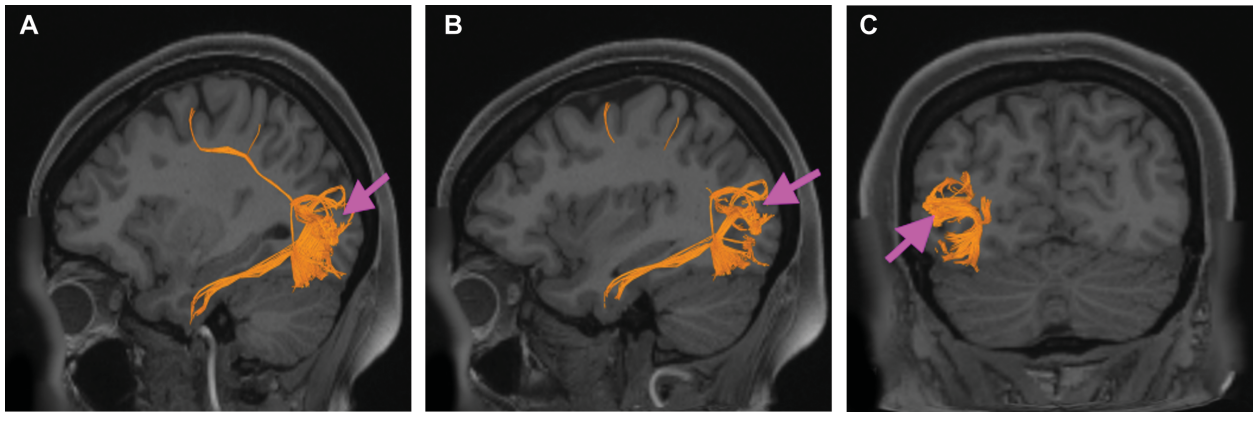

FIGURE 54. *Structural connectivity of MST in the left hemisphere, shown on T1-weighted MR images. Sagittal views of* **A**, *medial and* **B**, *lateral planes, and* **C**, *coronal view. Orange: white matter tracts of MST demonstrating connections with ILF.*

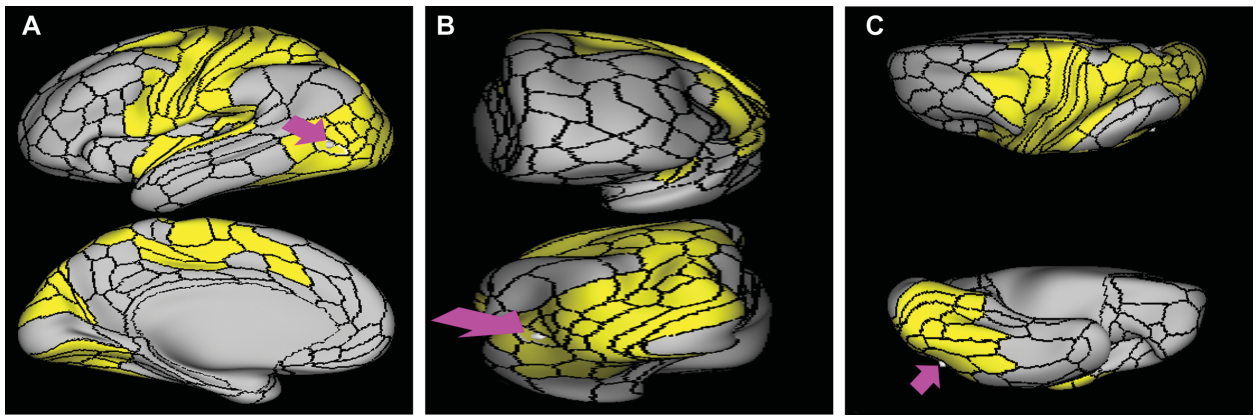

FIGURE 55. *Functional connectivity of FST demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation of interest.*

What are its borders? Area FST borders MST and V4t posteriorly, and PHT anteriorly. PH is its inferior border and TPOJ2 is its superior border.

What is its functional connectivity? Area FST demonstrates functional connectivity to areas 1, 2, 3a, and 3b in the sensory strip, area 4 in the motor strip, areas SCEF, FEF, PEF, 6mp, 6r, 6v, 6a, and 6d in the premotor region, areas 24dd, p32prime, 23c, and 5mv in the cingulate regions, areas FOP2, OP1, OP4, PFcm, PoI1, PoI2, 43, RI, LBelt, PBelt, and A4 in the insula and opercular region, areas TE2p and PHT in the temporal lobe, areas 7PC, 7AL, 7PL, 7am, PFt, PFop, PFm, AIP, VIP, LIPv, DVT, IP0, and IPS1 in the parietal lobe, areas V2, V3, and V4 in the medial occipital lobe, areas V3a, V3b, V7, V6, and V6a of the dorsal visual stream, areas FFC, VVC, V8, PIT, VMV1, VMV2, and VMV3 of the ventral visual stream, and areas TPOJ2, TPOJ3, MT, MST, V3cd, V4t, MT, LO1, LO2, LO3, and PH of the lateral occipital lobe (Figure 55).

What are its white matter connections? Area FST is structurally connected with the SLF and ILF. SLF projections are consistent and terminate at the premotor area at parcellation 8C. ILF projections are inconsistent. Short association bundles are connected to PHT, LO1, LO2, LO3, MST, MT PH, and V4 (Figure 56).

What is known about its function? Area FST acts as a major hub in the visual system, integrating massive amounts of visual information from both the dorsal and ventral streams. Area FST plays an integral role in the perception of image content by integrating detail, motion and form-sensitive information; processing of spatial reference frames leading to continuous global-motion perception and spatial map formation; and stimulus filtering due to heightened attention-based motion selectivity.[18,22]

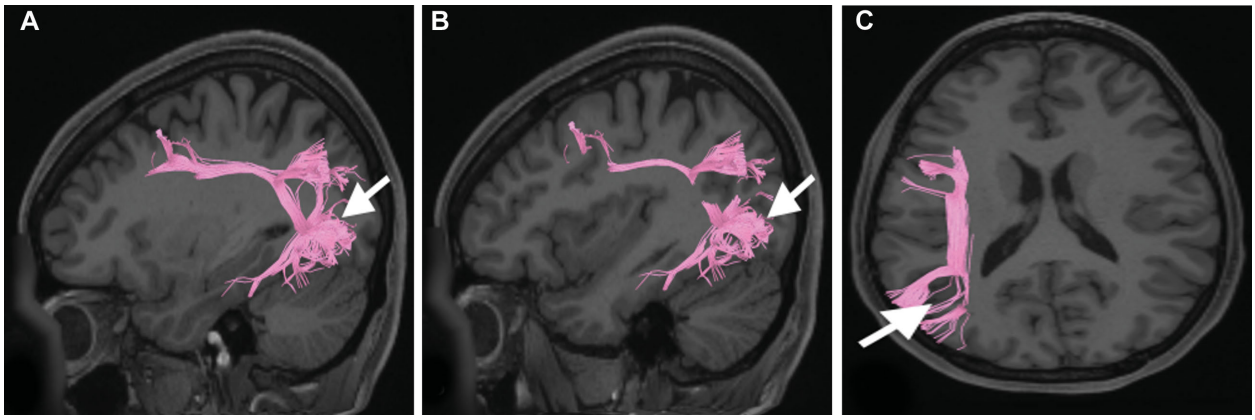

FIGURE 56. *Structural connectivity of FST in the left hemisphere, shown on T1-weighted MR images. Sagittal views of* **A**, *medial and* **B**, *lateral planes, and* **C**, *axial view. Pink: white matter tracts of FST demonstrating connections with SLF and ILF.*

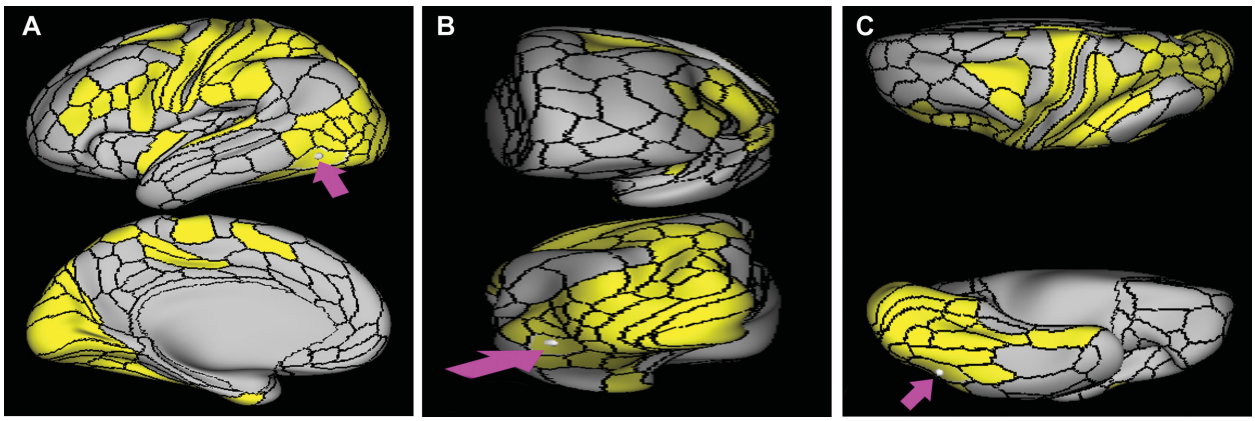

FIGURE 57. *Functional connectivity of PH demonstrated on an inflated left hemisphere.* **A**, *Lateral and medial views.* **B**, *Rostral and caudal views.* **C**, *Dorsal and ventral views. Parcellations with the strongest functional connectivity are shown in yellow. Pink arrows designate the parcellation of interest.*

Area PH

Where is it? Area PH is a horizontally oriented area in the anteroinferior lateral occipital lobe. It is roughly in line with the ITG and is mostly lateral to the occipito-temporal sulcus, which it forms a small portion of its lateral bank. Thus, it spills onto the basal surface slightly.

What are its borders? Area PH borders TE1p and TE2p anteriorly, and LO2 and PIT posteriorly. FFC is its medial neighbor on its basal surface. Its superior border is made up of parts of TE1p, PHT and FST.

What is its functional connectivity? Area PH demonstrates functional connectivity to areas 1, 2, and 3a in the sensory strip, area 4 in the motor strip, areas SCEF, FEF, PEF, 6r, 6v, and 6a, in the premotor region, areas p9-46v, IFSa, IFSp, IFJa, and IFjp in the lateral frontal lobe, areas 23c and 5mv in the cingulate regions, areas PoI2, LBelt, PBelt, and A4 in the insula and opercular region, areas PeEc, PHA3, TE2p, and PHT, in the temporal lobe, areas 7PC, 7PL, 7am, PGp, PFop, PF, AIP, MIP, VIP, LIPd, LIPv, DVT, IP2, IP0, and IPS1 in the parietal lobe, areas V1, V2, V3, and V4 in the medial occipital lobe, areas V3a, V3b, V7, V6, and V6a of the dorsal visual stream, areas FFC, VVC, V8, PIT, VMV1, VMV2, and VMV3 of the ventral visual stream, and areas TPOJ2, TPOJ3, MT, MST, V3cd, V4t, MT, LO1, LO2, LO3, and FST of the lateral occipital lobe (Figure 57).

What are its white matter connections? Area PH is structurally connected to the SLF and ILF. SLF projections are consistent across brains and terminate at 44 and 45. ILF projections are also

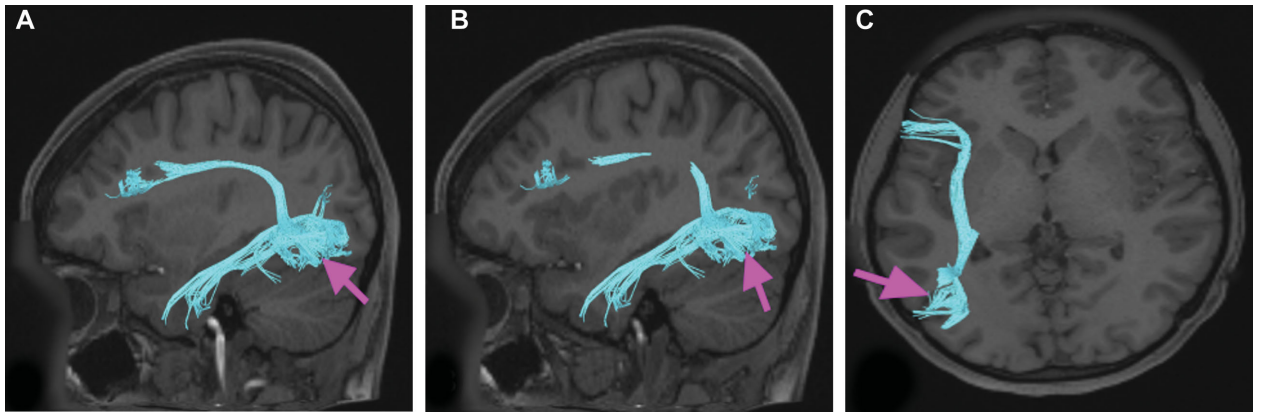

FIGURE 58. *Structural connectivity of PH in the left hemisphere, shown on T1-weighted MR images. Sagittal views of* **A**, *medial and* **B**, *lateral planes, and* **C**, *axial view. Gray: white matter tracts of PH demonstrating connections with SLF and ILF.*

consistent travel through the temporal lobe to end at TGv and TGd. Short association bundles are connected to FST, MST, MT, PHT, V4T, and TE1p (Figure 58).

What is known about its function? Area PH is a higher level holistic perception region of the visual system that acts as a hub of ventral stream input, integrating "place-specific" information, while showing little to no activity to objects or faces.[11,23] Using these data, area PH encodes a representation of the local scene and, due to its location, allows it to be remembered and subsequently recognized, implicating it in the formation of spatial maps, place encoding, and place recognition.[11,23]

DISCUSSION

To say that the human visual processing system is complicated is a massive understatement, as the seminal work in the area was begun decades ago and we are still mastering basic ideas in its organizational scheme. This chapter cannot resolve all of the outstanding questions related to human vision; however, what follows are some key observations about this area.

What Does Hierarchy Really Mean in this Part of the Brain?

We were taught in school that the visual system is the paradigmatic example of a serial processing network of increasingly refined steps. Information came from the thalamus in one format and entered V1 where its neurons would react to increasingly complex field patterns such as line orientation or color. This information is then passed in sequence to V2, V3, and so forth up the line of processing as fields become increasingly complex and specialized to create an image.

While the connectivity pattern of the visual system does not contradict this idea, it also suggests that the situation is a bit more complex than simple serial processing. Most notably, the early visual areas (V1, V2, and so on) are far too interconnected, especially to areas outside those involved in the visual network, for visual processing to occur as a simple chain of events. V1, as an example, demonstrates functional connectivity with a number of areas outside the visual system, and given that it contributes substantially to long distance tracts such as IFOF and MdLF, this is not surprising. Why such an early visual area would need direct physical connections to the lateral frontal lobe, and the regions of Heschl's gyrus is a fascinating question. Furthermore, all of the early visual areas have reciprocal connections with the posterior thalamus, namely the pulvinar.[24] Anatomically, these fibers course with the OR, so it is difficult to determine their function clinically, but it is remarkable that areas in such close proximity may also need to communicate with the thalamus in order to function properly.

So why do early visual areas need dense interconnections with the thalamus and with distant areas of the cortex? The answer is not entirely clear to us. However, we would speculate that some of these connections may allow areas to focus processing streams towards more salient visual areas as defined by the needs of other parts of the cortex, such as the frontal lobe. Computational modeling suggests that the visual system requires a winner-take-all regulation of attentional fields in order to work properly, given that the serial processing of each aspect of each visual pixel detectable by the human eye would probably require more neurons than are currently present in the human brain.[25] Either way, the blurring of lines between stages of the visual system is a fascinating observation revealed through connectomics.

The 2 Streams Rethought

Mishkin and Ungerleider[26] published a classic paper in 1982 based on their work regarding electrical stimulation in macaques that stated that the visual processing of objects and the processing for position of objects in visual space were segregated into two

processing streams, which they termed the "what" and the "where" pathways, also known as the dorsal and ventral streams. In humans, the areas that fit these roles are located far apart in physical space, as the ventral stream is located on the inferior (tentorial) surface of the occipital lobe, and the dorsal stream is located on the superior interhemispheric cleft. The data from humans strongly support the idea that positional and motion detection processing are located in the dorsal stream areas, and those involved in color and texture discrimination are located in the ventral stream areas.[27]

What is surprising is how densely interconnected these areas are with each other. A medium sized white matter tract, a relatively unknown pathway known as the vertical occipital fasciculus or VOF, is entirely dedicated to connecting these two streams at multiple points. In fact, almost every member of the ventral stream (FFC excluded) is connected to at least one member of the dorsal stream through the VOF. Why the visual system would segregate the processing of object recognition and spatial processing, but then densely interconnect them is a fascinating question. Notably, this tract is a long-range, en-passage type of connection, and does not seem to connect to any of the lateral occipital lobe regions between these two areas. Thus, as a long-range tract, the brain dedicated a significant amount of energy into making sure these streams interconnected with each other.

Long Distance Tract Anatomy

The occipital lobe's most notable features are the numerous white matter pathways that originate and terminate in the area. Our first efforts to map the connections of the visual system without a set of parcellations proved daunting, with numerous criss-crossing pathways coursing through the white matter. Most of the nonadjacent lobes of the brain are connected to occipital areas between the IFOF (frontal), ILF (anterior and inferior temporal), and the MdLF (temporal opercular and posterior temporal areas), with the previously mentioned VOF crossing all of them.

The key question for many of these tracts is why the brain would need these areas to be connected so much so that it would form extremely long, energetically costly connections in order to have these areas communicate. As an example, we provide a summary of the main connections of each tract below realizing this is somewhat of an oversimplification.

IFOF: connects the dorsal visual stream and early visual areas to the dorsolateral frontal lobe and parts of the medial premotor and orbitofrontal cortical regions.

ILF: connects parts of the ventral visual stream, early visual areas and lateral occipital processing areas to the anterior, inferior, and medial temporal lobe areas.

MdLF: connects the dorsal visual stream to auditory and semantic areas of the posterolateral temporal lobe.

VOF: connects the dorsal and ventral visual streams.

While we can hypothesize why the frontal lobe might need access to the visual processing areas (ie, redirection of attention for processing), it is difficult for us to come up with a plausible reason why the auditory areas need access to the dorsal stream as opposed to the ventral stream, or why the dorsal and ventral visual streams need to communicate with one another. These are key questions for future analysis in this area.

The Lateral Occipital Lobe

The lateral occipital lobe contains several well-known cortical areas for higher level visual processing, including MST and MT. It was thus a bit unexpected to find that this is one of the most modular parts of the human neocortex, meaning the areas mostly talk to each other and have few external connections save for the hub nodes that are most likely FST and PH. As for the other nodes in this region, save for a few parcellations, none of these areas give fibers to the numerous white matter pathways running through the occipital lobe. In addition, the functional connectivity is primarily to each other and other visual areas. The structural connectivity of these regions is largely local. FST and PH have far wider functional connectivity, and give fibers that connect widely to the SLF/arcuate complex, suggesting that these areas are the primary pathways whereby highly processed visual information enters the semantic network and its related areas. Whether these hubs represent the key point of connection between the semantic and visual systems is worth serious consideration, and the clinical and surgical implications of these observations are worth study.

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