Proposal for human visual pathway in the extrastriate cortex by fiber tracking method using diffusion-weighted MRI

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ABSTRACT

The extrastriate cortex in the human visual cortex is divided into two distinct clusters: the “what-information” processing area and the “where-information” processing area. It is widely accepted that the “what-information” cluster is processed through the ventral stream to the temporal cortex, and the “where-information” cluster through the dorsal stream to the parietal cortex. In human neuroanatomy, fiber bundles for the ventral stream (such as the inferior longitudinal fasciculus) are well defined, whereas fibers for the dorsal stream are poorly understood. In this study, we attempted to trace the dorsal stream fibers using a fiber tracking method using 7.0T diffusion-weighted MRI. We used data from a healthy male subject as well as from an unbiasedly selected nine-subject dataset in the Human Connectome Project. The surface of the visual area, including V1, V2, V3, V4, MT, was determined from the Brainnetome atlas (Fan et al., 2016), which is the connectivity-based parcellation framework of the human brain. The resulting visual pathway indicated that the putative pathway for the classical dorsal stream is unlikely to exist. Instead, we demonstrated that fiber connections exist between the angular gyrus and MT in the visual cortex, and between the angular gyrus and IT in the temporal cortex. Through that, we proposed a modified human visual pathway model based on our fiber tracking results in this report. The modified where-information pathway will provide a new aspect for the study of human visual processing.

1. Introduction

The human visual cortex can be divided into the striate cortex and extrastriate cortex. The striate cortex, or primary visual cortex (V1), in the occipital lobe is where the visual information is first delivered in the cerebral cortex. The visual information in the striate cortex is transmitted to the other high tier visual area, i.e., the extrastriate cortex. The extrastriate cortex, which consists of visual areas such as V2, V3, and V4 (Felleman and Essen, 1991; Kujovic et al., 2013), is roughly divided into the where-information (or how-information) and what-information processing areas (Goodale and Milner, 1992). The visual pathways that lead to the two visual areas in the extrastriate cortex are also independent, and the concept that “the dorsal stream mediates the where-information pathway, and the ventral stream mediates the what-information pathway” is widely accepted (Goodale and Milner, 1992; Mark et al., 2009; Michael et al., 2002). According to this two-streams hypothesis, the ventral stream area is mainly engaged in interpreting the properties of color, form, and objects. While, the dorsal stream area is mainly engaged in interpreting spatial organization, guiding action, and spatial attention (Michael et al., 2002).

In human neuroanatomy, fibers for the ventral stream, i.e., the inferior longitudinal fasciculus (ILF) and inferior fronto-occipital fasciculus (IFOF), are well defined; however, this is not the case for the fibers of the dorsal stream (Nolte, 2009; David and Anil, 2010; Adel and Ronald, 1998). Although there are possible connections to the dorsal area through U-fibers and through axonal connections within the cortex, studying the U-fibers in vivo is challenging methodologically.

Another issue is the middle temporal visual area (MT) or V5. MT is the essential relay structure in the classical dorsal stream and has been localized in several human studies with several methods (Sereno et al., 1995; Wandell et al., 2007; Glasser et al., 2016a; Fan et al., 2016; Malikovic et al., 2007; Zimmermann et al., 2011). However, the size and location of the human MT are not consistent among these studies. For example, the putative site of the human MT is in the inferior temporal
area in the visual field map (Sereno et al., 1995; Wandell et al., 2007), while in the multi-modal parcellation from Human Connectome Project (HCP), it is located in the middle temporal or occipital area (Glasser et al., 2016a). The problem is that if the MT is not in the superior temporal region, it is difficult for the dorsal stream model that transits through the MT to be functional.

The classical approach for tracing nerve fibers, such as the dorsal stream fibers, is a direct, invasive method using post-mortem tissue or cell analysis. The data from this approach can, to a degree, lead to conclusions, but since these are obtained from animal studies using primates or felines, there are fundamental limitations in applying these results to humans (Heiligenstetter and Jensen, 2016). Given the differences in the methods, terminology, and especially species, neural pathways such as the dorsal stream that are delineated from these historical neuroanatomy studies are not necessarily directly applicable to the human brain (Weiner et al., 2017).

In vivo human brain fiber tracking is available using advanced neuroimaging techniques, such as the diffusion-weighted imaging (DWI) using MRI. By using DWI and tractography techniques, we can estimate the fiber connectivity of the in vivo human brain (Basser et al., 1994). Particularly, advanced 7.0T MR-DWI based fiber tracking can now be used to analyze the fine fiber structure of the human white matter (Cho et al., 2015a, 2015b; Choi et al., 2018, 2019). Along with this brain imaging technique, the fiber tracking analysis using the advanced parcellated human cortex model can make the fiber tracking results less error-prone and more reliable to evaluate (Glasser et al., 2016a; Fan et al., 2016).

In this study, we traced the in vivo human visual pathway in the extrastriate cortex, including the dorsal stream fibers responsible for the where-information processing, using a fiber tracking method from the 7.0T MR-DWI. From the tracing results, we propose the responsible fiber bundle for where-information processing as the anterior part of the upper aspect of the occipital fasciculus (VOF) rather than a dorsal stream fiber structure.

2. Materials and methods

Three to four steps of the procedure were taken for this study depending on the analysis in question: acquisition of the DWI data, cortex parcellation and/or TDI data processing, and fiber tracking analysis.

2.1. MR data acquisition

We used the 7.0T MR-DWI data from unbiasedly selected subjects in the HCP data (Glasser et al., 2016b). The HCP data, which represented the most abundant and highest quality, is freely downloadable after verification at https://db.humanconnectome.org/app/template/SubjectDashboard.vm?project=HCP_1200&subjectGroupName=Subjects%20with%20T1%20MR%20Session%20Data). The DWI dataset was acquired using a 2D echo-planar imaging sequence with the following parameters: repetition time/echo time = 6000/83 ms; matrix size = 128 × 128 (FOV 230 mm × 45 slices); 1.8 mm isotropic resolution; 64 DW directions; b-value = 2000 s/mm², with a b = 0 image; GRAPPA with factor 3; and bandwidth of 1562 Hz/px. There were three repeats scanning with a total acquisition time of 19 min and 5 s.

2.2. TDI processing in a scanned MR dataset

The on-site scanned set of DWI data was processed using the track density imaging (TDI) image processing technique which provides more reliable and informative data about the white matter structure (Calamante et al., 2010, 2013). The TDI analysis was performed using MRtrix (Brain Research Institute, Florey Neuroscience Institutes, Melbourne, Australia, https://mrtrix.readthedocs.io/en/latest/) (Tournier et al., 2012). Relevant tracking parameters were: tracking type = SD_PROB; track minimum length = 20 mm; step-size = 0.02 mm; curvature radius constraint = 0.04 mm; Fiber Orientation Distribution (FOD) cutoff for track termination = 0.3; and number of tracks = 6,000,000 (Tournier et al., 2012). The final TDI image was generated with a nominal isotropic resolution of 0.18 mm.

2.3. Surface-based fiber tracking analysis for acquired 10 MR dataset

Before fiber tracking of the 10 subjects in the DWI dataset, we parcellated the cortex for surface-based fiber tracking analysis using the Brainnetome atlas (http://atlas.brainnetome.org) (Fan et al., 2016) and FreeSurfer software (https://surfer.nmr.mgh.harvard.edu/). The Brainnetome atlas is a parcellation framework of the human cortex based on the fiber connectivity model and Brodmann’s area (Brodmann, 1909; Fan et al., 2016). They identify the specific subdivisions of the entire human brain, with 210 cortical and 36 subcortical sub-regions. Supplementary Table 1 summarizes the label number and names of the parcellated Brainnetome brain areas in this study.

From the parcellated brain areas, the visual areas of interest in this study and label number of the Brainnetome area are as follow: V1 (96, 97), V2 (95, 100,102,103), V3 (104), V4 (98), MT (101), inferior temporal cortex (IT) (45, 47, 48, 50, 51), superior parietal lobule (SPL) (63, 64, 65, 66, 67, 74, 75), angular gyrus (ANG) (68,69,72), supramarginal gyrus (SMG) (70,71,73). We selected the Brainnetome area number according to the Brodmann’s area number (BAN) of the visual areas of interest: IT (BAN 20), ANG (BAN 39), SMG (BAN 40), and SPL (BAN 5, BAN 7) (BAN 39). The assigned MT area in the Brainnetome atlas was included in both the middle and inferior temporal areas.

Finally, the fiber tracking analysis was performed using MRtrix from the visual areas of interest such as the V1, V3, MT, ANG. With the fiber orientation distribution of the DWI data (Imax8), we set the fixed parameters in the fiber tracking for the entire dataset as follows: direction of the fiber tracking = uni-direction, step-size = 0.02 mm, curvature radius constraint = 0.04 mm, and extraction fiber number is 1000 from maximum 100000 generated fibers. The parameters for tracking directionality, step-size, curvature was settled based on previous papers (Cho et al., 2015a; Choi et al., 2018, 2019). The extracted fiber number for quantitative analysis (see Fig. 2) was fixed as 1000 in both hemispheres. The extracted fiber number for display (see Figs. 1, 3 and 4) was decided to be able to represent the fiber pathway effectively by ROI size and fiber-frequency in the given ROI, from the left hemisphere only.

Exceptionally, the cutoff value for track termination is determined empirically for each dataset due to varying signal levels of the selected MR-DWI data. The applied cutoff value of the on-site data is 0.5, and that of the other HCP data are 0.1, 0.07, 0.09, 0.1, 0.1, 0.09, 0.08, 0.09 with the ID order. The acquired DWI data and post-processed MRtrix data for the analysis in this study are available.
3. Results

3.1. Fiber tracking for dorsal and ventral stream fibers

First, we traced the fibers from V1 and V3 to confirm that there is no such fiber structure corresponding to the classical dorsal stream in the visual system. Fig. 1A and B shows the fiber tracking results from the seed position of V1 (blue) and V3 (green) of our on-site DWI data on the TDI image. As expected, according to traditional neuroanatomy, the fibers from V1 show the putative ventral stream clearly in the sagittal view (Fig. 1B), and ILF and IFOF in the axial view (Fig. 1A) (Rokem et al., 2017). The fibers from V3, however, do not show the putative dorsal stream in the sagittal view. We found that the connection to the SPL from both V1 and V3 are rare. Instead, the V3 fibers reach out towards the temporal area and V4.

3.2. Fiber tracking for the classical dorsal stream

Because fibers for the classical dorsal stream were not observed in the previous elementary fiber analysis step, we composed the where-information pathway in more detail according to the classical dorsal stream (see Fig. 5). Fig. 1C shows the composed fiber tracking results from our on-site scanned single subject data (see Supplementary Fig. 1 for other datasets). Each of the fiber bundles has a seed position and a waypoint mask. The paired seed position and waypoint mask for each colored fiber bundles are as follows: red (V1, V2), green (V2, V3), blue (V3, MT), yellow (MT, SPL).

In the classical approach, the dorsal stream from V1 passes through V3 and the MT. The tentative destination of the classical dorsal stream is the posterior parietal cortex (PPC) in the parietal cortex, and more specifically, the SPL (Glover, 2004). Note that another part of the PPC, the inferior parietal lobule (IPL), extends either ventral or lateral in the PPC. Contrary to expectations based on the classical dorsal stream model, however, the where-information pathway from V1 to the SPL is zigzag shape (magenta-colored arrow in Fig. 1C) instead of the round curve (cyan-colored arrow in Fig. 1C) in the result. The main reason for this distortion of the where-information pathway is likely due to the position of the MT. In this study, the assigned location of the MT by the brain parcellation is not in the superior part of the temporal gyrus, but instead is either middle or inferior.

3.3. Fiber tracking from MT and angular gyrus to the visual area

To determine the actual dorsal stream, we analyzed fiber connectivity from the MT. Fig. 2 shows our results of the fiber connectivity from 13 visual pathways of interest. The ratio of selected fibers to generated fibers indicates the relative portion of the fiber connection of interest from all the generated fibers in a particular visual area, such as the MT.

For example, “MT→V1” in Fig. 2 indicates the relative portion of the number of V1 fibers passing from the MT to the total number of MT fibers. We further identified the fiber-frequency, calculated as the ratio of extracted fibers to generated fibers of the MT (see Supplementary Fig. 2A). The absolute portion of the fiber connection from each ROI is the ratio of selected fibers to extracted fibers.

![Fig. 1. Fiber tracking results of the classical visual pathway of a single subject (our on-site scanned data) from left hemisphere on the TDI image. Axial view (A) and sagittal view (B) image of the fiber tracking result from seed position V1 (blue) and V3 (green) are shown. The generated fiber number from V1 and V3 in Figs. (A) and (B) are 10000 and 1000, respectively. (C) Sagittal view image of the fiber tracking result according to the classical dorsal pathway from maximum 100000 generated fibers in each seed position. The colors of each fiber bundle in Figs. (C) are as follows: V1→V2 (red), V2→V3 (green), V3→MT (blue), MT→SPL (yellow), and their conceptual trajectory is represented as a magenta-colored arrow in this figure. The cyan-colored arrow represents the putative pathway of the conventional dorsal stream. ILF, inferior longitudinal fasciculus; IFOF, inferior fronto-occipital fasciculus; MT, middle temporal visual area; SPL, superior parietal lobule.](Image 50x306 to 276x738)

![Fig. 2. The ratio of the selected fibers number to generated fibers number for each fibers from the 10-subject dataset. Error bars in each graph indicate the standard deviation. The bar of the left and right side in each fiber’s ratio data is the results of from left and right hemispheres, respectively. ANG, angular gyrus; IPL, inferior parietal lobule; IT, inferior temporal area; MT, middle temporal visual area; SMG, supramarginal gyrus; SPL, superior parietal lobule.](Image 318x589 to 546x738)
4. Discussion and conclusion

4.1. Considerations and limitations of the results

From this study, we provided evidence for non-classical connections of the where-information pathway in the visual system by a more direct approach using 7.0T MR tractography analysis. There are several considerations and limitations in these findings and the methods used. First, the false-positive possibility needs to be considered in the data interpretation of the fiber tracking study. Several recent studies have reported high false-positive rates in tractography studies (Maier-Hein et al., 2017). This is especially true for the fiber-frequency analysis per given region the MT to the SPL can be identified as MT→ANG→SPL, not MT→SPL.

3.4. Fiber tracking for the vertical occipital fasciculus and anterior vertical occipital fasciculus

The ANG is also connected with the IT, which is another major visual area in the ventral stream. Although the fiber connection between the ANG and the IT has been reported under several different names (discussed in detail later), we refer to this bundle as the anterior vertical occipital fasciculus (aVOF).

Fig. 3 shows fiber tracking of the aVOF from a single subject (our on-site scanned data) on the TDI image (indicated in magenta). The seed position and waypoint mask of the aVOF in this result are IT and ANG, respectively.

The cyan colored fiber bundle in Fig. 3 represents fiber tracking result of the VOF and perpendicular occipital fasciculus. The seed position and waypoint mask of this fiber bundle are V3 and V4, respectively. The VOF is a superior-inferior directional fasciculus in the occipital area, which is also known by several different names (Yeatman et al., 2014; Cho et al., 2015c). In the human brain, the VOF is a major white matter pathway between the dorsal and ventral visual cortex that connects V3 and V4 (Takemura et al., 2016). In the axial view (Fig. 3B), the patterns of the resulting VOF and aVOF fibers are highly consistent with those in previous reports (Takemura et al., 2016; Yeatman et al., 2014; Cho et al., 2015c) (see Supplementary Fig. 1 for other dataset, and Supplementary Fig. 4 for previous report).

3.5. 3-5. Reconstruction and proposal for visual pathway model

Fig. 4 shows fiber tracking of the main visual pathways in this study from another nine-subject HCP dataset on the MRI-TI image. This includes the major visual pathway in the extrastriate cortex, i.e., V1 fiber (blue), V3 fiber (green), VOF (yellow), aVOF (magenta), ANG→SPL (cyan). The IT→ANG→SPL pathway, the ventral stream from the V1 fiber, and the VOF and temporal connections from V3 fibers are shown consistent connectivity in this figure.

Finally, we composed a revised version of the classical visual pathway based on the results of the fiber tracking analysis in this study. Fig. 5 show the newly proposed visual pathway model. In the composed pathway, the pathway for the what-information is same as the classical visual model, but the pathway for the where-information differs in several points. In the classical model, the pathway to the SPL from the primary visual area passes via the dorsal stream, but in the modified model, it passes through the ANG with almost opposite direction. Furthermore, the fibers of the ANG are both connected with the V3 or MT and the IT. The resulting two pathways that pass through the ANG in the visual system using this fiber tracking technique, i.e., MT→ANG and IT→ANG, is consistent with the previous putative connectivity in the Separate visual representations (Glover, 2004). The IT→ANG formed another inter-stream connection between the dorsal-ventral streams, in the modified visual pathway. As a result, there is two inter-stream connection in the visual system: IT→ANG, i.e., aVOF, in the high-tier visual area and V4→V3→MT in the low-tier visual area, and we suggest the aVOF is also a visual processing fiber bundle, like the VOF.

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due to crossing fibers.

Even there is reflected the resting-state functional connectivity and hundreds of papers referred (Fan et al., 2016), the Brainnetome atlas is a group-based average of cortical regions. Therefore, this approach cannot account for variability between subjects in the definition of the visual areas. The parcellation error in the individual subject is inevitable using the atlas-based structural definitions. The intrinsic error seems one of the main reasons for the large variability between subjects in the fiber tracking structure (Fig. 4) and fiber tracking count (Fig. 2). To compensate for the parcellation error in the individual subject, we applied 10 subject data in this analysis.

4.2. About the fiber connection between ANG and IT: aVOF

Several reports describe the fiber connection between the ANG and the IT, i.e., the aVOF (Glover, 2004). Using a diffusion tensor tractography study, Kamali demonstrated the temporoparietal connection to the inferior parietal lobule (TP-IPL), which connects the inferior parietal lobule and temporoparietal cortex (Kamali et al., 2014). Seghier identified this fiber as the middle longitudinal fasciculus (MLF), which connects the ANG and the IT in the schematic illustration of the fiber bundles from ANG (Seghier, 2013). The author also mentions the arcuate fasciculus from Catani as a related fiber structure in their report.

The posterior segment of arcuate fasciculus (pAF) identified by Catani (2005) can also be considered as the aVOF. In the study that analyzed language networks in the human brain, the pAF was found to connect the Geschwind’s territory in the IPL and Wernicke’s territory in the temporal lobe (Catani et al., 2005). Furthermore, the pAF terminates on the right side of the IPL, i.e., the ANG. In the several individual data in this report, the fibers for Wernicke’s territory in pAF go to a more extended temporal area, i.e., the IT. Recently, Bullock demonstrated that the pAF and MLF as part of the dorso-ventral connective tracts in the posterior of the human brain (Bullock et al., 2019). Although the dorsal stream in this study is superior longitudinal fasciculus rather than a dorsal stream in the visual system, they are also based on HCP dataset in fiber tracking analysis to show the non-canonical associative tracts.

Wernicke and Obersteiner referred to the aVOF as the perpendicular fasciculus (FP) and fasciculus transversus occipitalis (OP), respectively (Yeatman et al., 2014). Wernicke identified the perpendicular fasciculus as the connection between the upper tip of the ANG with the fusiform gyrus (Yeatman et al., 2014; Wernicke, 1881). In the axial view, the passing position of the FP seems to be highly correlated with the position of the aVOF (see Supplementary Figs 4-5). Although it can be confusing to distinguish aVOF from VOF, as has been discussed previously (Weiner et al., 2017; Schurr et al., 2019), the VOF, which connects V3 and V4, is independent and obviously different from the aVOF, which connects the ANG and the IT. The difference is clearly shown in the sagittal and axial view (Fig. 3).

Finally, we concluded that the structure of the aVOF is the same as that of the FP from Wernicke’s, pAF from Catani’s, or MLF from Seghier’s reports. They described aVOF as a non-canonical associative tract or language-related track. Through a tractography-based approach, however, we demonstrated the critical role of the aVOF is processing the high-tier visual information with connections between the ventral visual streams and stream for where-information processing. Furthermore, we also concluded that the VOF from Yeatman’s study is the same structure as that of the fasciculus transversus occipitalis from Curran’s and the perpendicular fasciculus from Gray’s study (Yeatman et al., 2014).
4.3. Angular gyrus and visuospatial function

The putative destination of the where-information in the dorsal stream is the PPC. The primary role of the PPC is related to spatial reasoning related functions (Malhotra et al., 2009). Particularly in the proposed visual pathway model, the ANG in the IPL of the PPC is in the central area for where-information processing. The ANG also highly contributes to where-information processing, such as visuospatial representations (Seghier, 2013) and bottom-up attentional orienting (Shomstein, 2012). Therefore, the ANG is regarded as the where-information processing area in dorsal stream models (Glover, 2004; Rizzolatti and Matelli, 2003).

The ANG is also connected with the IT, the ventral stream area for what-information processing, via the aVOF. Therefore, the ANG actually has both what-information and where-information processing related roles, such as vigilance and salience detection (Singh and Husain, 2009). The function of the ANG includes the ability to read words, which is related to both language processing and visual skills (Seghier, 2013; Horwitz et al., 1998). The ANG may also be involved in mathematical ability, which may be the result of the interplay of linguistic competence and visuospatial representations (Dehaene et al., 1999).

4.4. Laterality of the fiber density in the visual system

With regard to the fiber ratio of the number of the selected fiber to generated fibers number, clear laterality between the left and right hemispheres was observed in this study (see Fig. 2). Except for the MT→V3, all the ratios of the major fiber data from the left hemisphere were larger than that from the right hemisphere. In the case of the fiber MT→→ANG, the ratio in the left hemisphere was twice the ratio in the right hemisphere. There is a possibility that the main reason for the ratio difference was from the laterality in fiber-frequency between hemispheres.

Considering the general ratio difference, between ratio differences for each fiber seems not so dramatically different in the left and right hemispheres. Nevertheless, several notable laterality information in the result may be used for the data interpretation in the functional laterality studies. For example, the V3→→ANG, ANG→→IT, and MT→→V3 in the right hemisphere are shown similar or bigger fiber ratio with the left hemisphere, in overall weakness.

In conclusion, we composed a where-information pathway by a systematic fiber tracking approach using the 7.0T MR-DWI data, and proposed a modified human visual pathway model based on our fiber tracking results in this report. There are three significant differences in this modified model. First, there is no dorsal stream fiber structure for where-information processing in the visual system. Second, there is a considerable fiber connection composing the visual system between the IT and ANG, i.e., aVOF. Third, the MT is connected to SPL via ANG, not directly. Hopefully, these modified where-information pathways will provide a new aspect for the study of human visual processing.

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Declaration of competing interest

The authors declare that they have no conflict of interest.

CRediT authorship contribution statement

Sang-Han Choi: Writing - original draft, Conceptualization, Formal analysis, Writing - original draft, Visualization, Data curation. Gangwon Jeong: Methodology, Software, Formal analysis. Young-Bo Kim: Validation, Visualization. Zang-Hee Cho: Methodology, Validation, Resources, Supervision, Project administration, Funding acquisition.

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Appendix A. Supplementary data

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