The Connectivity–Based Parcellation of The Angular Gyrus: Fiber Dissection And MR Tractography Study

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Abstract

The angular gyrus (AG) wraps the posterior end of the superior temporal sulcus (STS), so it is considered as a continuation of the superior/middle temporal gyrus and forms the inferior parietal lobule (IPL) with the supramarginal gyrus (SMG). The AG was functionally divided in the literature, but there is no fiber dissection study in this context. This study divided AG into superior (sAG) and inferior (iAG) parts by focusing on STS. Red blue silicone injected eight human cadaveric cerebrums were dissected via the Klingler method focusing on the AG. White matter (WM) tracts identified during dissection were then reconstructed on the Human Connectome Project 1065 individual template for validation. According to this study, superior longitudinal fasciculus (SLF) II and middle longitudinal fasciculus (MdLF) are associated with sAG; the anterior commissure (AC), optic radiation (OR) with iAG; the arcuate fasciculus (AF), inferior frontooccipital fasciculus (IFOF), and tapetum (Tp) with both parts. In cortical parcellation of AG based on STS, sAG and iAG were found to be associated with different fiber tracts. Although it has been shown in previous studies that there are functionally different subunits with AG parcellation, here, for the first time, different functions of the subunits have been revealed with cadaveric dissection and tractography images.

Introduction

The angular gyrus (AG) has extensive white matter (WM) connections with sensory and motor association cortices and classic language areas like the inferior frontal and superior temporal regions (Price 2015). It involves the semantic process, reading and comprehension, the default network, number processing, attention and spatial/social cognition, and reasoning (Seghier 2013). It also shows robust activation across a range of tasks proposed to engage the episodic memory system, simulating possible events in the future and remembering events from the past (Ramanan 2018). The AG is located at the junction of the temporal, parietal, and occipital lobes (Seghier 2013). It can be identified with its horseshoe shape near the dorsal-posterior segment of the superior temporal sulcus (STS) (Naidich et al. 1995). It wraps the posterior end of the STS (Rhoton 2007) and forms the inferior parietal lobule (IPL) with the supramarginal gyrus (SMG) (Binder et al. 2009). The AG was functionally divided by different authors (Seghier et al. 2010; Wang et al. 2012; Seghier 2013; Wang et al. 2017); however, there is no fiber dissection study in this context. This study aims to examine possible functional differences based on WM connectivity differences between the superior and inferior parts of the angular gyrus.

Methods

Preparation of Specimens

Red, blue silicone injected eight human cadaveric cerebrums, fixed in 5% formalin for two months and then frozen at -10°C for 15 days, were defrosted and preserved at room temperature. Lateral hemispheric dissection was performed with the Klingler method, focusing on superior and inferior parietal lobule. All

fiber tracts adjacent to the AG were dissected and synchronous MR tractography images were given stepwise.

Division of the AG

The AG is divided into two parts by their position to STS in this study. The upper front part was named superior angular gyrus (sAG), and the lower back part was named inferior angular gyrus (iAG). The analyses of the dissections were focused on the differences between the sAG and iAG. AG-related fiber tracts were classified as associated with sAG, iAG, or both (Table 1).

Fiber tracking

All fiber tracking was performed with DSI-Studio (<http://dsi-studio.labsolver.org>). A group average template was constructed from a total of 1065 subjects from the Human Connectome Project, which is publically available at <http://dsi-studio.labsolver.org>. A multishell diffusion scheme was used, and the b-values were 990, 1985, and 2980 s/mm². The number of diffusion sampling directions was 90, 90, and 90, respectively. The in-plane resolution was 1.25 mm, and the slice thickness was 1.25 mm. The diffusion data were reconstructed in the Montreal Neurological Institute space using q-space diffeomorphic reconstruction (Yeh and Tseng 2011) to obtain the spin distribution function (Yeh et al. 2010). A diffusion sampling length ratio of 2.5 was used, and the output resolution was 2 mm. The restricted diffusion was quantified using restricted diffusion imaging (Yeh et al. 2017). A deterministic fiber tracking algorithm (Yeh et al. 2013) was used. Fiber tracking was initiated following selected regions of interest placement on the quantitative anisotropy map until 100,000 streamlines were detected. Fiber progression continued with an anisotropy threshold of 0.156, the angular threshold of 45 to 60 depending on the fiber tract, and step size was randomly selected from 0.5 to 1.5 voxels. Tracks with a length shorter than 30 or longer than 300 mm were discarded. False or overlapping tracts that did not correspond to the tract of interest were manually deleted. Fiber tract tracts were validated by comparison with the conventional magnetic resonance images over which reconstructed tracts were displayed and fiber dissection images. Fiber tracking and validation were performed by a radiologist with three years of fiber-tracking analysis experience.

Results

To be able to orient the surface anatomy and the AG, the following anatomical structures were identified in the first step: central sulcus, pre/postcentral gyrus, postcentral sulcus, intraparietal sulcus, Sylvian fissure, and STS. The area behind the postcentral sulcus is divided by the intraparietal sulcus into the superior parietal lobule (SPL) and IPL. The IPL consists of the SMG and AG (Cikla et al. 2016). The structures that wrap the posterior end of the Sylvian fissure and the STS are described as SMG and AG, respectively (Rhoton 2007). The AG, limited by descending portion of the intermediate sulcus of Jensen anteriorly (Ribas 2010) and by the dorsal part of the anterior occipital sulcus posteriorly (Rademacher 1992). These sulci demarcate the AG from SMG and occipital lobe, respectively. (Fig. 1a, b).

The dissection was performed on the lateral surface of the hemisphere. The cortical gray matter of the inferior frontal gyrus (IFG)/middle frontal gyrus (MFG), the inferior part of the pre/postcentral gyrus, the SMG/AG, and the superior temporal gyrus (STG)/middle temporal gyrus (MTG) and U fibers were removed. Superior longitudinal fasciculus (SLF) II/III, arcuate fasciculus (AF), and middle longitudinal fasciculus (MdLF) were revealed. SLF III lies inferior and lateral to SLF II, and there is no clear demarcation between these structures. The connections between the AG-MFG/IFG and the SMG-IFG are provided by SLF II and III, respectively. AF wraps around the posterior edge of the insula like a horseshoe and establishes the connection between the middle/superior temporal gyri and inferior/middle frontal gyri. The MdLF connects the temporal pole and STG to the angular gyrus and superior occipital lobe (Güngör et al. 2017). Our dissections indicate that the SLF II lies between the MFG and sAG and has no connections with the iAG. On the other hand, the SLF III starting from IFG, terminates at SMG and does not give fiber branches to AG. However, the dorsal part of the AF creates a similar shape to the AG and has connections with both sAG and iAG. (Fig. 1c, d)

Dissection of the temporal lobes grey matter and U fibers exposed the MdLF fibers. The MdLF projects a straight route from the temporal pole to the superior parietal lobule above the STS. Therefore, while MdLF fibers have connections with sAG and not iAG. After the MdLF fibers emerge from the STG, they merge with the sagittal stratum (SS) fibers. SS fibers are located medial to the AF/SLF complex and lateral to the tapetal fibers of the atrium (Di Carlo et al. 2019). Corona Radiata (CR) and SS were revealed when the dissection was deepened on the lateral aspect of the hemisphere, keeping the SLF II and AF as a strip. Removing the insular grey matter exposed the extreme capsule (ExC). After removing ExC, the claustrum at the apex of the insula and the inferior frontooccipital fasciculus (IFOF) were revealed in the limen insula (Yakar et al. 2018). (Fig. 1e, f)

The IFOF courses medial to the MdLF, starting from the inferior and middle frontal gyri and extending through the temporal, occipital lobes, and the superior parietal lobule (Martino 2010). According to the dissections and tractography analyses, IFOF reaches the sAG and iAG both. When the superficial dorsal fibers of IFOF pass through the sAG, the deep ventral fibers pass through the iAG. The vascular structures retracted to present the IFOF and MdLF more clearly. After removing IFOF, the uncinate fasciculus (UF) was exposed (Fig. 1g, h). The UF passes just under the IFOF and connects orbitofrontal/septal areas to the anterior part of the temporal lobe. The IFOF and UF form the ventral portion of the external capsule (EC) (Ribas et al. 2018).

The strip of SLF II and AF was removed, and the internal capsule (IC) fibers were exposed at a depth of dissection along the CR. The CR fibers (fan-shaped, projection fibers between the cerebral cortex, brainstem, and spinal cord) were inferiorly converged as IC. Deep temporal dissection revealed the anterior commissure (AC) fibers and the thalamus. The AC consists of a body and anterior/posterior crura. The body of AC crosses midline at the anterior wall of the third ventricle and divides into anterior/posterior crura. The posterior crura give extensions to temporal and occipital lobes (Güngör et al. 2017). The occipital extension of the AC travels lateral to the temporal horn and atrium. Our analyses support that the AC fibers travel through the iAG below the sAG. (Fig. 1g, h) Removing the AC fibers

exposes the optic radiation (Egemen et al. 2021). It has been reported that optic radiation consists of 3 subgroups of fibers. The anterior fibers of the optic radiation (OR) pass through the lateral aspect of the temporal horn and the floor of the atrium (Güngör et al. 2017). Our analyses support these previous findings. In addition, our dissection demonstrates a relationship between the iAG and the OR by following these fibers in the posterior route. The last stage of our dissection reveals tapetum (Tp) fibers between the OR and the lateral ventricle (Pastor-Escartín et al. 2019). Tp fibers surround the lateral wall and the roof of the atrium, occipital and temporal horns of the lateral ventricles. Our observations show the Tp fibers run deep in sAG and iAG. (Fig. 1i, j)

SLF II, III, IC, UF, and Th were preserved in a different hemisphere until the last stage. When the SS and AC fibers were removed, the OR and Meyer loop were revealed. In addition, the roof, lateral wall, and one-third of the lateral part of the floor of the temporal horn were covered by OR fibers. Finally, by removing the CR fibers, the Tp structure surrounding the atrium, occipital and temporal horn of the lateral ventricle was revealed (Fig. 1i, j).

Discussion

The WM anatomy of the temporal, parietal, occipital lobe (Burks et al. 2017; Kadri et al. 2017; Ripollés et al. 2017; Saalasti et al. 2019; Jitsuishi and Yamaguchi 2020; Briggs et al. 2021; Egemen et al. 2021) and junction (Biceroglu et al. 2019) has been extensively studied in the literature. Previously, Yagmurlu et al. (2015) divided AG as upper and lower parts with evaluating only the SLF II and AF. In our study, the AG was divided into two parts (superior and inferior), and the WM fibers associated with its parts were compared. Consequently, SLF II and MdLF are associated with sAG; the AC, OR with iAG; the AF, IFOF, and Tp with both parts. To the best of our knowledge, this is the first anatomical study dividing the AG into two parts to evaluate all fiber tracts according to these parts.

A functional MRI study (Seghier et al. 2010) divided left AG into three parts: mid, dorsomedial, and ventrolateral regions. It has been stated that regardless of the presence of the stimulus, the mid-region is involved in semantic associations, the dorsomedial region is in search of semantics in all visual stimulations, and the ventrolateral region is in the conceptual identification of visual inputs. According to the anatomical classification in our study, approximately the dorsomedial region corresponds to sAG and the ventrolateral and mid-region to iAG. A tractography-based parcellation study divided IPL into five clusters (Mars et al. 2011). The activity was recorded when people redirected visuospatial attention from one location to another in tractography corresponding to the anterior part of AG and when people successfully retrieved memories in the posterior part of AG. The classification in this study was not correlated with the classification in our study. In another study (Wang et al. 2017), AG was parcelled as dorsal and ventral parts. The dorsal part had associations with the frontal pole, superior frontal gyrus, MFG, pre-supplementary motor area, middle MTG, and dorsal lateral prefrontal cortex (DLPFC). The ventral part had associations with DLPFC, anterior MTG, precuneus, medial prefrontal cortex, anterior and posterior parahippocampus. In the tractography-based study conducted by Wang et al. (2012), IPL was divided into 5 clusters, but the cluster containing AG was also included the ventral premotor cortex and

IFG. All these studies in the literature evaluated AG as functional, but our study is the first to classify AG according to cortical anatomy and determine the WM connections of sAG and IAG in detail.

There is no agreement in the terminology of SLF. The frontoparietal network was first classified as SLF I, II, and III by Petrides and Pandya (1984). There are publications stating that SLF is a single entity (Christiaens et al. 2015; Lerma-Usabiaga et al. 2019), or that questioning the existence of SLF I (Wang et al. 2016), or that SLF II and III are entirely independent entities from SLF I (Komaitis et al. 2019). Furthermore, the clear distinction between SLF and AF has not been resolved yet (Schurr et al. 2020). Besides, Nakajima et al. (2019) proposed classification as ventral SLF (SLF III, AF anterior), dorsal SLF (SLF II), posterior SLF (SLF-temporoparietal segment and AF posterior), and AF (AF long fibers). In a recent study (Schurr et al. 2020), SLF II and III boundaries were tried to be separated in tractography using three different datasets. They focused on SLF III and pointed that the SLF III projects to AG, especially in the right hemisphere. They didn't divide AG into parts; however, the SLF III covers only the sAG on their tractographic demonstrations. In contrast, we didn't notice any connections between SLF III and the AG based on our dissections. The classically defined SLF II relationship with sAG and iAG has not been noted so far. Recent publications (Nakajima et al. 2019; Schurr et al. 2020) and our findings reveal that SLF II is associated with sAG. Because of SLF II affects oculomotor function and spatial aspects, Gerstmann syndrome and Spatial hemineglect are observed in its disconnection (Chechlacz et al. 2013; Yagmurlu et al. 2015). (Table 2) The AF connects STG and MTG to MFG and IFG and therefore is in direct contact with both parts of AG.

While fiber dissection studies have shown that the parietal connections of the MdLF are almost completely terminated at the SPL (Maldonado et al. 2013; Wang et al. 2013), DTI studies have also shown connections to the IPL (Menjot de Champfleur et al. 2013, Makris et al. 2017). In current studies, MdLF has been divided into many different functional units, but the AG was considered a single unit (Latini et al. 2021; Makris et al. 2017; Kalyvas et al. 2020). A recent study (Latini et al. 2021) divided the MdLF into anterior (deeper brunch) and posterior (superficial branch) parts. Anterior MdLF connects anterior STG and planum polare. Posterior MdLF connects posterior STG, anterior transverse temporal gyrus, planum temporale, and the parieto-occipital region. For the first time in the literature, it has been described that when the AG is divided into two parts, the MdLF fibers progress at the level of the superior AG and form the roof of the iAG. MdLF takes part in processing the spatial features of sounds, but the disconnection syndrome is unknown (Wang et al. 2013; Güngör et al. 2017). (Table 2)

The IFOF originates in parietal and occipital lobes and terminates in the inferior frontal lobe (Motomura et al. 2014). Adjacent to the inferolateral insula, the IFOF courses along with the UF (Kier et al. 2004). Based on its relationship with the central insular sulcus, the IFOF is divided into two parts: anterior and posterior (Güngör et al. 2017). To reach the occipital lobe, the anterior part runs lateral to the inferior of frontal horn, and the posterior part runs lateral to the temporal horn and inferior to the atrium. The anterior and posterior parts run roughly deep into the sAG and iAG. The IFOF takes part in lexical-semantic and visual spatial processing. The disconnection of IFOF fibers include semantic paraphasias and nonword reading (Duffau et al. 2005; Rollans et al. 2017). (Table 2)

The OR fibers lie deep to the AC and SS fibers and courses lateral to the temporal horn and inferior two-thirds of the atrium. The OR fibers will be at the iAG level when evaluated according to the cortical surface. The Tp, consisting of splenial callosal fibers surrounding the lateral wall and roof of the atrium, and occipital and temporal horns, is located between the ventricular ependyma and the OR fibers (Yakar et al. 2018). Tp fibers run deep in both parts of the AG. The functions and disconnection syndromes of all relevant fibers to AG are summarized in Table 2.

In conclusion, AG was divided into sAG and iAG based on STS in this study. Although it has been shown in previous studies that there are functionally different subunits with AG parcellation, here, for the first time, different functions of the subunits have been revealed with cadaveric dissection and tractography images. Therefore, in surgical interventions for AG, this parcellation of AG will be more efficacious in predicting related complications.

Declarations

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Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

Ethics approval

This study was performed in line with the principles of the Declaration of Helsinki. Approval was granted by the

Ethics Committee of Pamukkale University (Date: 30.11.2021/No: 21).

Data availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

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Tables

Table 1 Fiber tracts related to sAG, iAG, or both. (sAG: superior Angular Gyrus, iAG: inferior Angular Gyrus, SLF II: Superior Longitudinal Fasciculus II, AF: Arcuate Fasciculus; MdLF: Middle Longitudinal Fasciculus, IFOF: Inferior Frontooccipital Fasciculus, AC: Anterior Commissure, OR: Optic Radiation, Tp: Tapetum)

Fibers	sAG	iAG	Both
SLF II	+		
AF			+
MdLF	+		
IFOF			+
AC		+	
OR		+	
Tp			+

Table 2 The functions of the fibers relevant to AG. (AG: Angular Gyrus, SLF II: Superior Longitudinal Fasciculus II, AF: Arcuate Fasciculus; MdLF: Middle Longitudinal Fasciculus, IFOF: Inferior Frontooccipital

Fasciculus, AC: Anterior Commissure, OR: Optic Radiation, Tp: Tapetum)

Fibers	Function	Disconnection syndrome
SLF II (Chechlacz et al. 2013; Yagmurlu et al. 2015)	Oculomotor and aspects of spatial function	Gerstmann syndrome, Spatial hemineglect
AF (Vassal et al. 2013; Chan-Seng et al. 2014; Yagmurlu et al. 2016; Güngör et al. 2017)	Lexical, semantic, and phonological language	Transcortical motor aphasia
	processing	Phonological paraphasia
		Repetition disorder aphasia
MdLF (Wang et al. 2013; Güngör et al. 2017)	Processing the spatial features of sounds	Unknown
IFOF (Duffau et al. 2005; Rollans et al. 2017)	Lexical-semantic processing	Semantic paraphasias
	Visual spatial processing	Orthography-phonology translation (nonword reading)
AC (Yagmurlu et al. 2015; Güngör et al. 2017)	Olfactory, auditory, and visual communication	Verbal anosmia
OR (Benjamin et al. 2014; Yagmurlu et al. 2015; Güngör et al. 2017)	Visual	Anterior part: superior homonymous quadrantanopsia
		Posterior part: homonymous inferior quadrantanopia
		Central part: macular visual defects
Tp (Pustina et al. 2014; Güngör et al. 2017; Yakar et al. 2018)	Goal-directed actions	Contralateral epileptiform activities
		Auditory or visual disconnection syndromes

Figures

Figure 1

Fiber pathways associated with the angular gyrus are demonstrated by fiber dissection and tractography images. **a** Superficial cortical and vascular anatomy on a red-blue silicone injected cadaveric head. **b** The projection of the angular gyrus demonstrated on the MR tractography image. **c** MdLF and SLF II pass through sAG, AF pass through both sAG and iAG. **d** The pathways shown in 1c are presented on the tractography. **e** IFOF fibers pass through both the sAG and the iAG. **f** The course of IFOF fibers and their relationship with MdLF and SLF II is presented on tractography. **g** AC fibers do not pass through the sAG while passing through the iAG in the occipital projection. **h** The relation of AC fibers with iAG is shown on the tractography image. **i** A non-silicone-injected hemisphere is presented within the cadaveric skull in the previous figures to preserve anatomical orientation. **j** OR fibers pass through the iAG only, and tapetum fibers pass through both angular gyrus segments. sAG, superior angular gyrus; iAG, inferior angular gyrus; SLF, superior longitudinal fasciculus; MdLF, middle longitudinal fasciculus; AF, arcuate fasciculus; IFOF, inferior frontooccipital fasciculus; UF, uncinate fasciculus; AC, anterior commissure; OR, optic radiation.