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The perisylvian language network and language analytical abilities

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ABSTRACT: Aiming at exploring the brain's structural organisation underlying successful second language learning, we investigate the anatomy of the perisylvian language network in a group of healthy adults, consisting of participants with high and average language analytical abilities. Utilising deterministic tractography, six tracts per participant (left and right long direct segment, left and right indirect anterior segment and left and right indirect posterior segment) were virtually dissected and measurements pertaining to their microstructural organisation were collected. Our results obtained by means of linear discriminant analysis pointed to mean diffusivity (MD) values of three tracts (right anterior, left long and left anterior segments) as best discriminating between the two groups. By far the highest coefficient was obtained for the MD values of the right anterior segment, pointing to the role of the right white matter fronto-parietal connectivity for superior language learning abilities. The results imply the importance of attentional processes and reasoning abilities for successful L2 acquisition, and support previous findings concerning right-hemispheric involvement in language learning.

1. Introduction

The brain's structural connectivity underpinning the uniquely human language function has in recent years gained increased attention in the field of cognitive neuroscience and neurobiology of language. The anatomical organisation of language-specific white matter connections (e.g., Catani et al., 2007; Catani, Jones, & Ffytche, 2005), their development (e.g., Mohades et al., 2015), and functional contributions (e.g., López-Barroso et al., 2013; Vaquero, Rodríguez-Fornells, & Reiterer, 2016) have been studied with the overarching aim of producing a coherent understanding of how the brain networks shape our communicative behaviour. Central to such studies is the perisylvian language network (also referred to as the arcuate fasciculus) comprising of three white matter fibre tracts: the long segment running dorsally from the frontal lobe ("Broca's region") to temporal structures comprising Wernicke's area, the anterior segment connecting "Broca's region" with the inferior parietal cortex (in particular the angular gyrus), and the posterior segment connecting the inferior parietal lobe to "Wernicke's territory" (Catani et al., 2005).

Adult second language (L2) learning is an aspect of our linguistic behaviour characterised by a lack of uniformity in results. Although when acquiring languages as children we tend to reach universally high levels of proficiency, mastering an L2 after the onset of puberty seems virtually unattainable (Abrahamsson & Hyltenstam, 2009). One factor mitigating this age effect is language aptitude (Abrahamsson & Hyltenstam, 2008; DeKeyser, 2000), a specific talent for L2 learning, exhibiting considerable variation between learners (Dörnyei & Skehan, 2003). Language aptitude consists of several components, tapping into

various sub-processes of language learning. For example, rote-learning memory underlies lexico-semantic processing, and language analytical abilities (LAA) determine successful morphosyntactic and grammatical processing (see e.g., Li, 2016). In terms of neural correlates of the different components of language aptitude, previous research from our group suggests that engagement of the right hemisphere (through activity localised both in the frontal and parietal sites) might lie at the centre of individual differences in abilities for L2 grammar learning (Kepinska, de Rover, Caspers, & Schiller, 2017; Kepinska, Pereda, Caspers, & Schiller, under review). This finding is in line with the suggestion that right hemispheric involvement in language learning relates to L2 learning rate (Prat, Yamasaki, Kluender, & Stocco, 2016).

The goal of the present study is to investigate the structure of the perisylvian language network in participants who differ in their language analytical abilities. We aim to employ diffusion tensor imaging (DTI) and deterministic tractography in order to reproduce anatomical features of the language pathways of the participants. DTI tractography measures diffusivity of water along different directions, and offers visualisation of white matter pathways by inferring the movement of water molecules exposed to a magnetic gradient (Catani & Mesulam, 2008, see also Le Bihan, 2003). Moreover, it quantifies the microstructural tissue properties underlying the distinguished pathways, enabling comparisons between individuals and establishment of functional correlates of the particular anatomical structures.

Our approach is partly based on a recently proposed neuroanatomical model for Social Communication And Language Evolution and Development (SCALED), in which Catani and Bambini (2014) outline how the hierarchically organised aspects of social communication map onto the major structural networks of the human brain. The model distinguishes five levels of language and communicative functions: (1) informative actions, (2) communicative intentions, (3) lexical and semantic processing, (4) syntactic analysis and (5) pragmatic integration, and couples each function with a separate anatomically defined network. The perisylvian language pathways are the core anatomical structures behind the identified processes, and according to the model, syntactic analysis is proposed to be supported by the direct fronto-temporal long segment pathway. If this particular tract plays a prominent role in successful syntactic processing, its structure should correspond with individuals' abilities for acquiring novel morphosyntactic information (hypothesis 1). Another possibility is that our previous functional neuroimaging and neurophysiological (fMRI and EEG) results point to the right anterior structures as possibly underlying the differences in language analytical abilities (hypothesis 2). By investigating the brain anatomy of participants with different levels of LAA, we aim at gaining insights into the brain's structural connectivity correlates of successful L2 learning. Furthermore, on the basis of the SCALED model, we postulate that involvement of left-hemispheric structures (in particular the direct fronto-temporal long segment pathway) would point to LAA being coupled with more efficient syntactic analysis processing in both L1 and L2. Right anterior involvement would mean that LAA is more specific to L2 learning, and does not necessarily translate into better L1 processing.

2. Methods

2.1. Participants

Forty-two healthy adults (32 female, age 19-43, $M = 23.38$ years) with no contra-indications for an MRI scan took part in the study. They were recruited on the basis of a test of language analytical abilities (LLAMA_F, Meara, 2005) administered to a large group of participants ($N = 307$). The study cohort comprised two groups based on the LLAMA_F scores: participants who gained an “average score” (i.e. 30-50¹, $M = 44.00$, $SD = 8.82$; Average LAA group), and participants who gained an “outstandingly good” score (i.e. 80-100, $M = 89.09$, $SD = 8.11$; High LAA group). There were 20 Average LAA participants (16 female), age 19-39 years ($M = 23.60$ years) and 22 High LAA participants (16 female), age 19-43 years ($M = 23.18$ years). All were native speakers of Dutch, right-handed and had normal or corrected-to-normal vision (see also Kepinska et al., 2017).

The Medical Ethical Committee of the Leiden University Medical Centre (LUMC) (Leiden, the Netherlands) approved the protocol of the MRI experiment; behavioural testing was also conducted according to the Ethics Code of the Faculty of Humanities at Leiden University. Participants gave written informed consent prior to the experiment and were remunerated for their time.

2.2. DTI data acquisition and processing

DTI images were acquired on a Philips 3T MR-system (Best, The Netherlands) located at the Leiden University Medical Centre (LUMC) equipped with a SENSE-32 channel head coil. Each scan consisted of 32 diffusion-weighted images, and one non-diffusion weighted volume (b-value 1000 s/mm²). Matrix size was 112 x 112 x 60; voxel size was 2 x 2 x 2.1 mm. The data were pre-processed and corrected for eddy current and motion artefacts using ExploreDTI (www.exploredti.org). Whole-brain deterministic tractography was performed from all brain voxels with fractional anisotropy >0.2. Streamlines were propagated with a step-size of 0.5 mm. The maximum curvature threshold was set to 35°. Where fractional anisotropy was <0.2 or when the angle between two consecutive tractography steps was >35°, tractography stopped. Finally, diffusion tensor maps and whole brain tractography were exported to Trackvis (Wang, Benner, Sorensen, & Wedeen, 2007) for virtual manual dissection of the tracts.

Tractography dissections were obtained for the three perisylvian language networks in both hemispheres (six tracts per dataset were virtually dissected²). All dissections were performed in participants’ native space with a two regions of interest (ROIs) approach as described by Catani, Howard, Pajevic, and Jones (2002) and Catani et al. (2005), and adopted by e.g. Catani et al. (2007), Forkel et al. (2014), López-Barroso et al. (2013) and Vaquero et al. (2016). Additionally, since detailed instructions are available for a one ROI approach for tractography dissection of the whole arcuate fasciculus (AF) (Catani & Thiebaut de Schotten, 2008), we further guided the placement of the frontal and temporal ROIs by first

¹ Although the LLAMA manual defines “average score” as 25-45, a score of 50 was also included as average in this study. The scores are awarded at intervals of 10 and a score of 45 is not possible to obtain. Therefore, there were no participants who scored 25, either.

² With the exception of the right long segment in case of two participants (one from the High and one from the Average LAA group), whose direct white matter connection between the frontal and temporal ROIs was fully left-lateralised (see e.g., Catani et al., 2007 for similar findings).

dissecting the whole AF with a one ROI approach. Visualising all its fibres enabled us to accurately determine the position of the frontal and temporal ROIs in such a way that as many relevant fibres as possible were included in the dissected tracts. The parietal ROI was drawn as last. Here, first fibres originating in the frontal and temporal ROI were visualised, ensuring that all fibres passing between the frontal and the parietal ROIs, and between the temporal and the parietal ROIs were included in the distinguished tracts. Finally, artefactual fibres³ were removed using exclusion ROIs. All datasets were carefully inspected by two dissectors, with special care taken for consistency of the distinguished tracts across all participants. The individual dissections for all data sets are presented in the Supplementary Material.

2.3. Statistical analysis

Per tract three measurements were used in the subsequent statistical analysis: fractional anisotropy (FA), mean diffusivity (MD) and volume (in cm³). FA and MD are diffusion parameters describing the average microstructural tissue properties along the segmented tracts. FA is used as a measure of microstructural integrity of white matter, putatively following from the degree of myelination or axonal density (Johansen-Berg & Behrens, 2009); the higher the FA values, the denser the given tract. MD describes microscopic water movement without directional preferences; the higher its values, the more free water diffusion along a tract (Soares, Marques, Alves, & Sousa, 2013), and the less dense the tissue.

Our aim in the statistical analysis was to investigate how the micro-structure of the perisylvian language network differs in participants with average language analytical ability versus those with high language analytical ability. Given the study cohort comprising two distinguished groups regarding their LAA scores, we conducted a linear discriminant analysis using the MASS package (Venables & Ripley, 2002) in R (R Development Core Team, 2015), treating the different tract measurements (FA, MD and volume) as predictors (i.e., 6 tracts x 3 measurements = 18 predictors) and LAA group as the outcome variable. Our goal was to establish which part of the variability present in the data set is systematically related to the grouping. Linear discriminant analysis (LDA) derives the linear combination of predictors that best separates the groups (i.e., small difference within but large differences between groups in the given measurement) that are given by the outcome variable and provides discriminant weights, which are coefficients that indicate the strength of the contribution of each predictor to the linear function. Considering the small size of our data set, our goal was constrained to the exploration of the main relations present in the data only.

In the first pre-processing stage for the analysis, all values at each of the six tracts were standardized to have zero mean and unit variance over all participants. In order to maximise the availability of data for LDA, we imputed mean scores for four cells which had missing data values (MD and FA values in case of the absent right long segment in two data sets).

3. Results

The linear discriminant function, when evaluated on the same data set, displayed a mean classification accuracy of 78% (78% correctly classified as High LAA and

³ The artefactual fibres were defined as fibres: fibres constituting the long or anterior AF segment running anteriorly and superiorly to “Broca’s territory” (cf. Catani, Jones, & Ffytche, 2005); fibres crossing to the contralateral hemisphere; fibres terminating medially from the main arcuate bundle.

79% correctly classified as Average LAA), with a precision rate of 0.82 (i.e., the fraction of all positive tests that are true positives) and a recall rate of 0.78 (i.e., the true positive rate). Table 1 shows the discriminant weights associated with the first – most important – linear function for each predictor included in the LDA. As can be seen in the list of coefficients, the MD measures contributed most to discrimination between average and high LAA groups. The most influential predictor in the linear discriminant function is Right Anterior MD (2.29), followed by Left Long MD (-1.49) and Left Anterior MD (-0.96). All other predictors had coefficients between -0.49 and 0.73. Figure 1 compares MD measurements between the two LAA groups in each of the six tracts.

AF segment	Measure	Linear discriminant coefficient
Left Long	FA	0.18
	MD	-1.49
	Volume	-0.42
Left Anterior	FA	-0.11
	MD	-0.96
	Volume	-0.17
Left Posterior	FA	0.00
	MD	-0.32
	Volume	0.73
Right Long	FA	-0.28
	MD	0.03
	Volume	-0.03
Right Anterior	FA	-0.44
	MD	2.29
	Volume	-0.20
Right Posterior	FA	-0.49
	MD	0.52
	Volume	0.31

Table 1 Results of the LDA listing the linear discriminant coefficients for all measures (FA, MD and volume) of the six dissected tracts.

Guided by the LDA results, we furthermore performed a series of independent samples t-tests, investigating whether the Average LAA group had significantly higher values of the MD measures determined as the most influential predictors (Right Anterior MD, Left Long MD and Left Anterior MD). The test was significant for MD values of the right anterior AF segment only ($t(40) = -2.153$, $p = 0.019$, one-tailed) and not significant for the left long AF segment ($t(40) = -0.898$, $p = 0.187$, one-tailed), or the left anterior AF segment ($t(40) = -0.807$, $p = 0.212$, one-tailed).

4. Discussion

The goal of the present experiment was to investigate the structure of the perisylvian language networks of participants with different levels of language analytical abilities. DTI images of two groups (High and Average LAA) were collected and deterministic tractography of three segments of the AF was performed bilaterally. Per participant six tracts were dissected: left and right long direct segment, left and right indirect anterior segment and left and right indirect posterior segment. Each tract was quantified by means of three measurements: FA, MD and volume. Our statistical analysis aimed at determining the best predictors of the group membership among the collected measurements, and at

pointing to the structural network bearing most importance for one’s analytical abilities for language learning. On the basis of the SCALED model (Catani & Bambini, 2014), we expected the long direct segment of the AF to be the strongest group membership predictor; meanwhile, our previous fMRI and EEG data suggested the right anterior indirect pathway as a possible white matter correlate of different LAA levels.

Out of all tractography-based measurements of the dissected pathways, the MD values of the right indirect anterior segment of the arcuate fasciculus predicted the group membership of our participants the strongest. They were followed by MD values of the left long and anterior segments. The linear discriminant analysis thus offered support for the predictions based on our previous functional data (Kepinska et al., 2017, under review), and to some extent to the predictions of the SCALED model (Catani & Bambini, 2014).

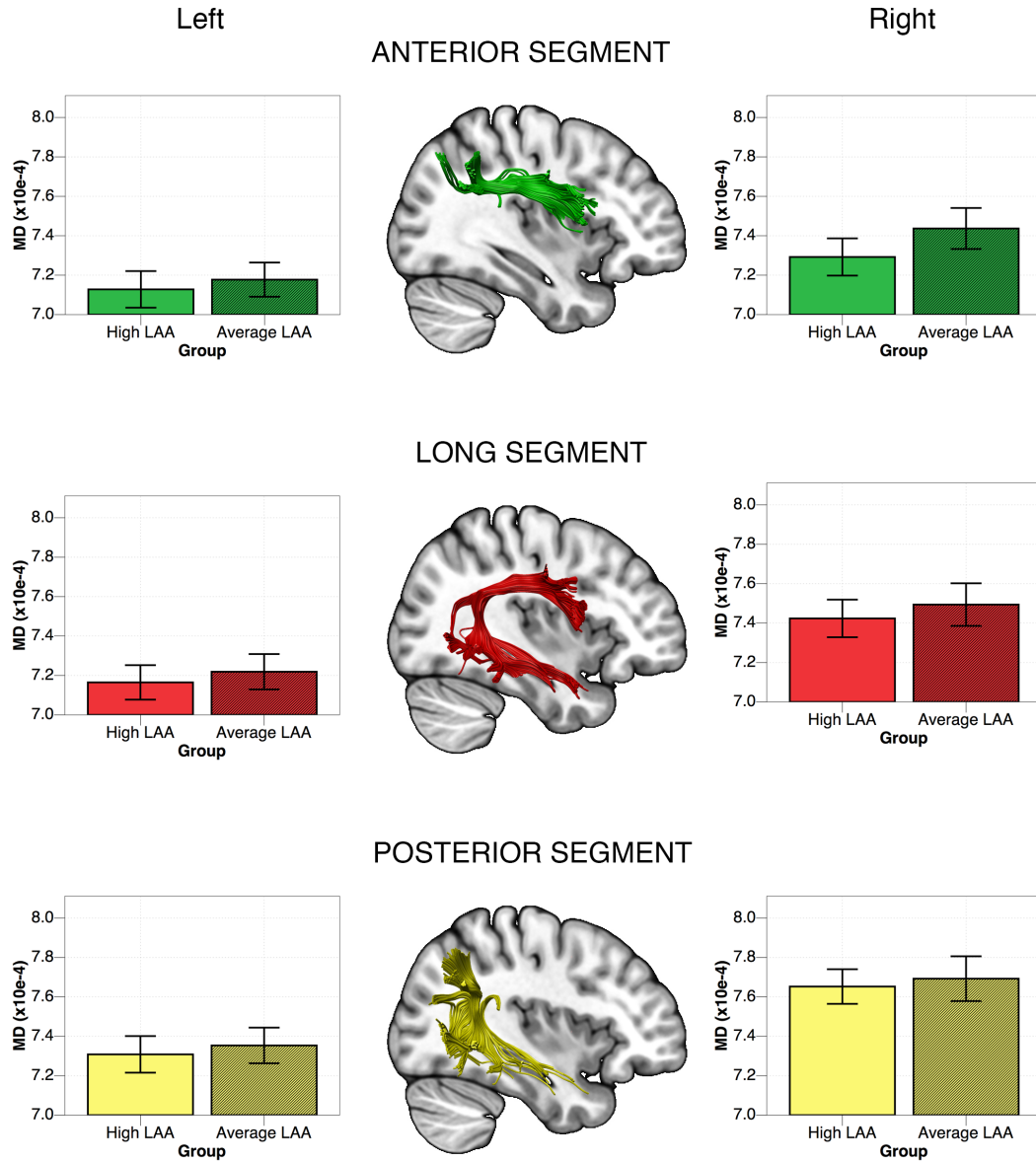


Figure 1 MD of the six dissected tracts for the High and Average LAA groups. According to the LDA, values of the right anterior segment predicted group membership the strongest, followed by values of the left long segment and the left anterior segment.

MD is a measure of the overall amount of water diffusion, and has been associated with the degree of myelination, coherence of fibres and the amount of crossing fibres from other bundles (Jones, Knösche, & Turner, 2013). Kronfeld-Duenias, Amir, Ezrati-Vinacour, Civier, and Ben-Shachar (2016) interpreted lower MD values as underlying faster transmission between cortical regions, a view following from studies relating low MD to enhanced processing speed. The present results indicate that MD values of three segments of the perisylvian language network were best at differentiating between highly and moderately skilled language learners. In particular, the lower MD values of the right anterior segment for the High LAA as compared to the Average LAA participants suggest that better language analytical abilities can be associated with a more coherent organisation and/or denser tissue microstructure of white matter tracts, possibly resulting in a

more efficient information transfer between the separate cortical regions. What exact biological factors underlie this result, is – given the available methodology – an open question.

The contribution of the microstructural architecture of the long segment of the AF to participants' classification can be traced back to its proposed involvement in syntactic analysis (Catani & Bambini, 2014), and the evidence for its relation to language learning abilities in other domains (López-Barroso et al., 2013; Vaquero et al., 2016). The functional role of the fronto-parietal white matter connections has been proposed to be coupled with attentional processes (De Diego-Balaguer, Martinez-Alvarez, & Pons, 2016) thanks to which visual and auditory percepts turn into relevant information (Catani & Bambini, 2014). Jung and Haier (2007) postulated interactions between frontal and parietal association cortices to underpin individual differences in reasoning abilities. This notion seems to be in line with the suggestion of Skehan (1998) about a relationship between language learning abilities and intelligence, which is particularly strong for the analytical abilities (cf. Biedron & Pawlak, 2016; Li, 2016). From an evolutionary point of view, Schoenemann, Sheehan and Glotzer (2005) underscored the importance of white matter connections between the prefrontal cortex and posterior regions for the development of higher cognition, in particular language skills. This view seems to be in line with language acquisition experiments, in which fronto-parietal activity patterns and interactions are a well-established finding. Aside from our previous studies mentioned above, they were previously described by Tettamanti et al. (2002) who reported bilateral dorso- and ventrolateral prefrontal, and parietal cortical activations to acquisition of natural language syntax; Fletcher, Büchel, Josephs, Friston and Dolan (1999) noted a bilateral fronto-parietal network in an artificial grammar learning paradigm. Recently, Goranskaya, Kreitewolf, Mueller, Friederici and Hartwigsen (2016) pointed to the fronto-parietal network as one orchestrating successful artificial grammar learning.

Our results are furthermore in line with findings concerning right-hemispheric white matter pathways predicting Mandarin learning success (Qi, Han, Garel, San Chen, & Gabrieli, 2015). The structures established as underlying individual differences in L2 attainment were partly overlapping with the ones found in the present study, i.e. the right fronto-parietal connection. Qi et al. (2015) offered an interpretation of white matter connectivity in the right hemisphere underlying successful L2 learning as being driven by its involvement in prosodic processing and L2 learning in general. However, as Qi et al. investigated language learning success, it might be that their findings could at least in part be related to superior language analytical abilities of the learners, as is the case for the present data. In a similar vein, right-hemispheric white matter integrity of the lower parietal regions has been shown to be important for pitch related novel grammar learning (Loui, Li, & Schlaug, 2011) and suggested to be a marker of neurobiological differences in learning abilities.

In terms of limitations, it is important to note that given the size of our data set, the present study is exploratory in nature. Translation of its results to further applications can be achieved by means of a larger study with a cross-validation procedure enabling formulation of predictions for new participants (cf. Gabrieli, Ghosh, & Whitfield-Gabrieli, 2015). Furthermore, we want to point out that the decomposition of the arcuate fasciculus implemented in the present study is by no means the only possible virtual dissection approach, but one of many (see Friederici, 2009 for an overview). Moreover, since the placement of our seed regions was guided by the dissection of the whole AF from its middle part, we did

not in detail investigate its exact cortical terminations sites (cf. Bernal & Altman, 2010). Given the debates concerning both the terminations and the decomposition of the AF (see e.g. Bernal & Altman, 2010; Brown et al., 2014; Glasser & Rilling, 2008), the detailed anatomy of the AF undoubtedly merits further investigations.

5. Conclusion

The present results provide insights into the brain's structural underpinnings of inter-individual differences in the ability to discern and learn novel morphosyntactic rules. Our statistical analysis shows that microstructural properties the right fronto-parietal language pathways (i.e. the anterior indirect segment of the arcuate fasciculus) contribute the strongest to the discrimination between two groups of participants highly differing in their language analytical abilities. The results underscore the role of the right white matter fronto-parietal connectivity for superior language learning abilities, hint at the importance of attentional processes and reasoning abilities for successful L2 acquisition, and support previous findings concerning right-hemispheric involvement in language learning.

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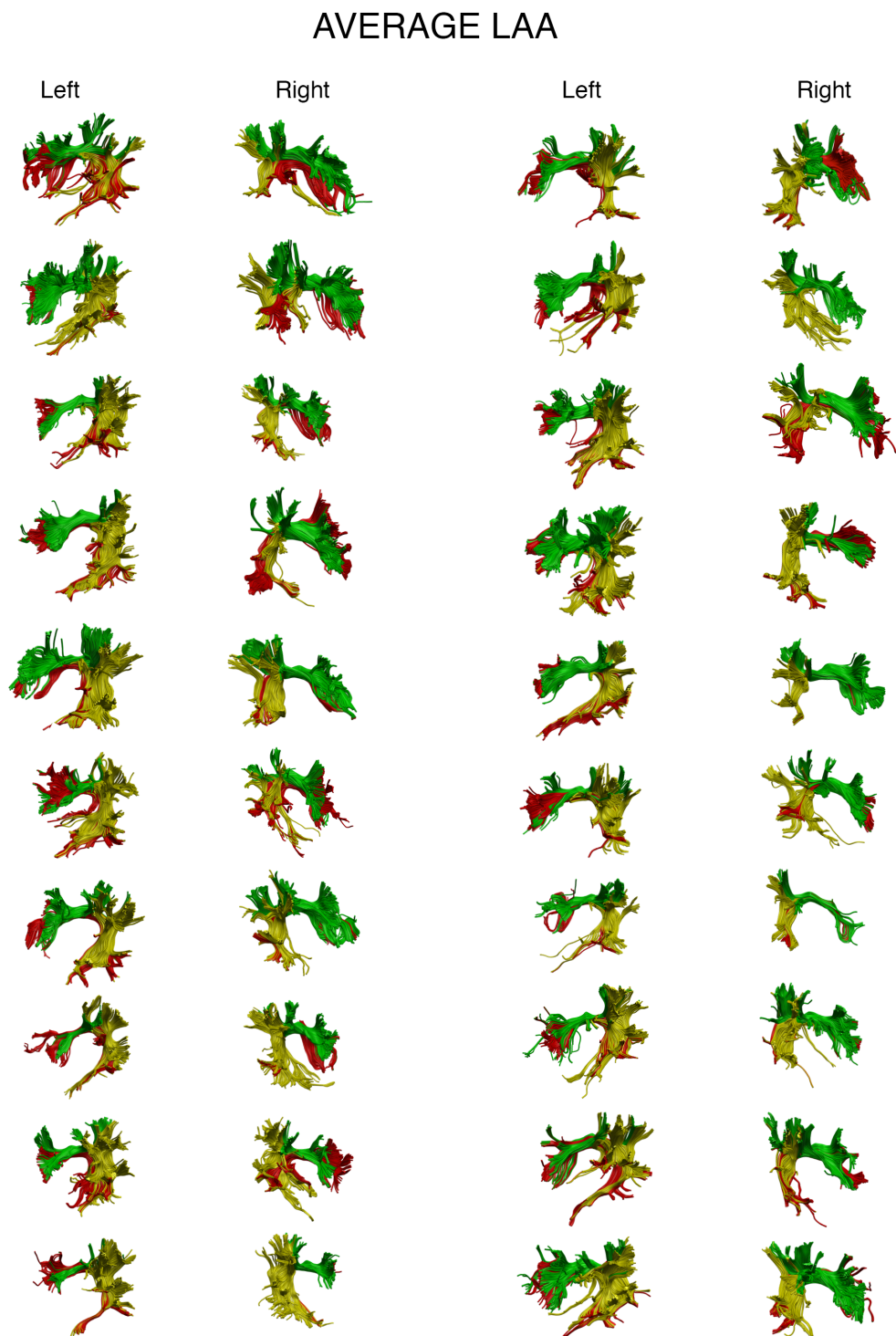
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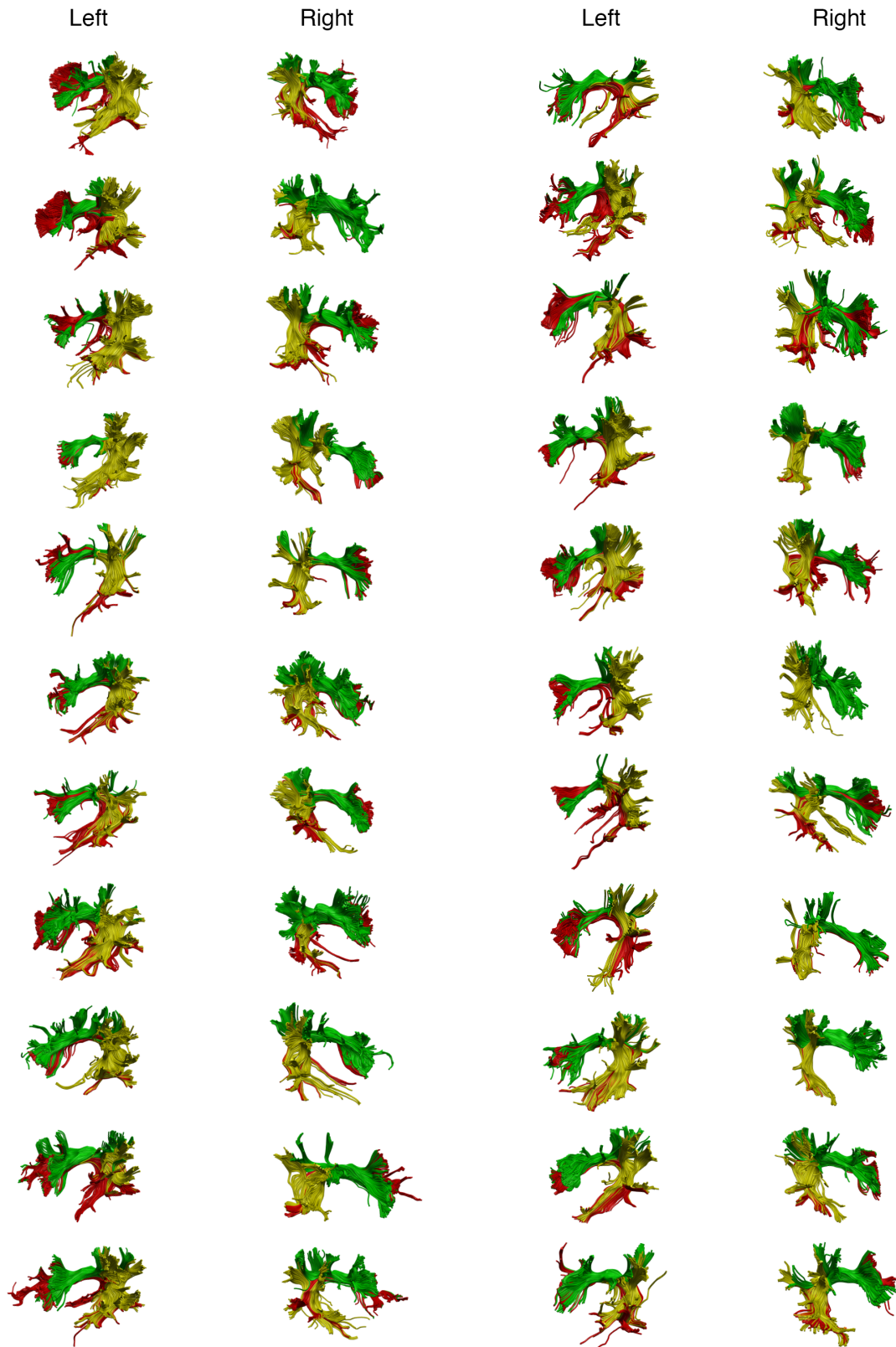
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8. Supplementary material



Supplementary Figure 1 Individual dissections of the bilateral AF from Average LAA participants.

HIGH LAA



Supplementary Figure 2 Individual dissections of the bilateral AF from High LAA participants.