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Frontoparietal anatomical connectivity predicts second language learning success

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<u>Abstract</u>

There is considerable individual variability in second language (L2) learning abilities in adulthood. The inferior parietal lobule, important in L2 learning success, is anatomically connected to language areas in the frontal lobe via the superior longitudinal fasciculus (SLF). The second and third branches of the SLF (SLF II and III) have not been examined separately in the context of language, yet are known to have dissociable frontoparietal connections. Studying these pathways and their functional contributions to L2 learning is thus of great interest. Using diffusion MRI tractography, we investigated individuals undergoing language training to explore brain structural predictors of L2 learning success. We dissected SLF II and III using gold-standard anatomical definitions, and related pre-learning white matter integrity to language improvement in lexical retrieval, while SLF III properties predicted improvement in articulation rate. Finer-grained separation of these pathways enables better understanding of their distinct roles in language, which is essential for studying how anatomical connectivity relates to L2 learning abilities.

Keywords: individual differences; inferior parietal lobule; neural biomarkers; superior longitudinal fasciculus; tractography

Second language acquisition, specifically during adulthood, is a challenging process in comparison with native language acquisition (see Birdsong 2018 for review). It is known that there is considerable inter-individual variability in second language (L2) learning abilities (Sparks et al. 1998; Golestani and Zatorre 2009; Jakoby et al. 2011), which has previously been shown to relate to functional and structural brain connectivity within both hemispheres (López-Barroso et al. 2013; Ocklenburg et al. 2014; Qi et al. 2015; Chai et al. 2016). In addition to the classical posterior temporal and inferior frontal language processing areas, the inferior parietal lobule (IPL) has been investigated in relation to language learning and has even been described as a "location for multilingual talent" (Della Rosa et al. 2013). Specifically, L2 learning and proficiency have been related to the structure of the IPL in terms of grey matter (GM) density (Mechelli et al. 2004; Grogan et al. 2012), white matter (WM) density (Golestani and Pallier 2007) and functional involvement in learning-related changes (Cornelissen et al. 2004; Barbeau et al. 2017). The IPL comprises the supramarginal gyrus (SMG) and the angular gyrus (AG), which have specific and distinct WM anatomical connectivity with language regions in the frontal lobe (Petrides and Pandya 1984; 2009; Barbeau et al. 2020). However, to date, these specific connections have not been examined in relation to language learning and proficiency. It is, therefore, of great interest to study the different fronto-parietal pathways originating from the IPL to elucidate their particular functional contributions to specific aspects of individual L2 learning abilities.

The main WM tract that connects the IPL to frontal regions is the Superior Longitudinal Fasciculus (SLF). A recurring difficulty in the study of the SLF and language is that its frontoparietal trajectory is in close proximity to that of another major WM pathway involved in language, the Arcuate Fasciculus (AF), which connects ventrolateral frontal areas, or the classic Broca's area, to the posterior Superior Temporal Gyrus (pSTG), i.e. the classic Wernicke's area. This anatomical proximity makes the separation of these pathways difficult in the human brain using available methods, and given the focus on the AF in the literature because it connects the classical language areas, these pathways are frequently amalgamated. Indeed, many studies refer to this WM system as the AF/SLF (Dick and Tremblay 2012). This has led to a relative neglect of the study of the function of the SLF (Dick and Tremblay 2012; Gierhan 2013; Tremblay and Dick 2016), and although previous work has already anatomically distinguished the AF from the SLF in the human brain (Makris et al. 2005; Frey et al. 2008; Thiebaut de Schotten et al. 2012; Kamali et al. 2014; Barbeau et al. 2020), their anatomical and functional descriptions remain inconsistent between studies. Issues related to the separation of the tracts come mainly from the limitations of the technique used, diffusion MRI (dMRI), with which the main direction of major pathways can easily be demonstrated, but not the precise origin and termination of the tracts (Martino et al. 2011; Campbell and Pike 2014); in addition, determining whether connections are monosynaptic (i.e. direct) or polysynaptic is impossible. Thus, the gold standard remains the use of anatomical tracers in the macaque monkey, allowing the precise axonal origin, course, and terminations of tracts to be established. In the context of language, invasive studies in monkey models remain relevant because the existence of cytoarchitectonically homologous areas to the human language areas have been demonstrated (Petrides and Pandya 2002; Petrides et al. 2005; Petrides 2014). Thus, a priori knowledge of exact anatomical connectivity in nonhuman primate brains can inform in vivo studies in the human brain using dMRI (Campbell and Pike 2014; Schilling et al. 2020). The anatomical studies in macaque monkeys have provided precise connectivity information about cortical areas that, in the left hemisphere of the human brain, are known to be involved in language processes. Such approaches have allowed investigators to establish that not only do frontal areas have distinct connections to posterior temporal areas through the AF and to the IPL via the SLF, but also that the SLF itself can be divided into three separate branches (Petrides and Pandya 1984). In these autoradiographic studies in monkeys, it has been shown that a specific branch of the SLF, i.e. SLF II, connects the caudal IPL, homologue of the AG in the human

brain, to ventrolateral frontal area 45 and area 8a which plays a role in regulating attention (Petrides and Pandya 1984; Petrides and Pandya 2006; Petrides 2015). By contrast, another branch of the SLF, i.e. SLF III, originates from the rostral IPL, homologue of the SMG, and links it with area 44 (pars opercularis), ventral orofacial premotor area 6 which controls the orofacial musculature, and area 9/46v, which is involved in the articulatory loop of working memory (Petrides and Pandya 1984; Petrides and Pandya 2006; Petrides and Pandya 2009; Petrides 2014; Petrides 2015). Both tracts of interest in the present investigation are considered part of the dorsal stream within the framework of Hickok and Poeppel (2004). We have examined the involvement of SLF II (from the angular gyrus) and SLF III (from the supramarginal gyrus) in language processing. Previous studies in human subjects had separated SLF II from SLF III using dMRI (Makris et al. 2005; Galantucci et al. 2011; Kamali et al. 2014; Wang et al. 2016; Barbeau et al. 2020; Schurr et al. 2020) and resting state functional connectivity (Kelly et al. 2010; Margulies and Petrides 2013; Jakobsen et al. 2016), but the definitions of SLF II and III across studies have not always been consistent with each other. Thus, there remains much uncertainty surrounding the anatomy and functional role of these WM pathways in language (Makris et al. 2005; Kellmeyer et al. 2013; Nakajima et al. 2020).

Nonetheless, a few studies have suggested differential roles for these pathways in language. Involvement of SLF III in the articulatory aspects of language has previously been suggested (Kellmeyer et al. 2013; Duffau et al. 2014; Nakajima et al. 2020). Note that SLF III links the orofacial portion of premotor area 6 and area 44 (Broca's area) with the SMG, namely areas implicated in speech production and articulatory planning (Heim et al. 2009; Papoutsi et al. 2009; Price 2010; Bouchard et al. 2013; Oberhuber et al. 2016). By contrast, the role of SLF II is less clear, but its involvement in language seems evident based on its connections to area 45 of the IFG, and the fact that the AG is also thought to play an important role in language processing. It has been suggested that SLF II may be implicated in functional aspects, such as verbal working memory (Nakajima et al. 2020), semantic retrieval (Madhavan et al. 2014), and action naming (Akinina et al. 2019). This proposed role for SLF II in retrieval is consistent with proposals relating to functional contributions of the brain regions it connects. Indeed, both area 45 (Klein et al. 1995; Petrides et al. 1995; Petrides 2002; Heim et al. 2009) and the AG (Seghier 2012; Herbet et al. 2016; Linden et al. 2017) have been shown to be involved in the retrieval of information from memory. Based on this evidence, in the context of L2 learning, we hypothesise that SLF II facilitates retrieval of vocabulary from memory but SLF III mediates planning and the articulatory aspects of speech in the new language. Thus, distinguishing SLF II and III from each other may allow us to determine their differential roles in language and how these distinct fasciculi relate to individual L2 learning abilities.

In the present study, we sought to differentiate the roles of SLF II and SLF III in L2 learning by investigating how structural connectivity to the AG part of the IPL via SLF II and the SMG part via SLF III is associated with specific improvements in aspects of L2 that are related to the hypothesised functions of these WM tracts. One of the strengths of the study is the validity of our SLF II and III dissections, which are based on anatomical definitions from macaque tracer studies and comparative cytoarchitectonic analyses of the origins of the pathways (Petrides and Pandya 1984; Petrides and Pandya 2002), thus enabling accurate examination of their functional distinctions related to second language acquisition. Based on theorised involvement of SLF II in lexical retrieval and of SLF III in articulatory aspects of language, we focus on improvements in L2 vocabulary and articulation rate, respectively. We hypothesised that measures of WM properties of SLF II would be related to vocabulary acquisition, while SLF III WM properties would be related to improvements in articulation rate.

<u>Methods</u>

Participants

Eighteen participants (mean age 20.8 ± 3.9 years, 12 females) were recruited from a French language learning course. All participants were right-handed and had normal or corrected-tonormal vision, and reported no hearing impairments, history of traumatic brain injury, neurological disorders, or conditions incompatible with MRI scanning. Individuals with advanced musical training were excluded because of the known link between musical training and language ability (see Milovanov and Tervaniemi 2011 and Jäncke 2012 for review). Ten participants out of the 18 had American English as their native (L1) language (English group) and eight were native Mandarin speakers (Mandarin group) with English as their L2. Recruitment was focused on speakers of these languages because they constituted the largest, most homogeneous groups of eligible participants. Individuals with high proficiency in languages other than English or Mandarin were excluded. The groups were matched on working memory and general intelligence (Table 1), as measured by the Digit Span, Letter-Number Sequencing and Matrix Reasoning subtests of the WAIS-IV (Wechsler Adult Intelligence Scale; Wechsler 2008). No group differences in behavioural measures in English or French or in WM integrity measures were found pre- or post- language training and, therefore, we treated the participants as a single group for all analyses. All participants were students at McGill University, studying in English, and were considered beginner learners of French at the start of the study, which was approved by the Research Ethics Board of the Montreal Neurological Institute (MNI); the participants gave informed written consent.

<Table 1>

French learning course

The French learning course was a tertiary-level course for beginners offered by the McGill French Language Centre. Participants received approximately 80 hours of training over one or two semesters, focusing on various aspects of language, such as grammar, writing, comprehension, and discussion of both audio and visual documents to develop their competency in multiple domains.

Language tasks

The participants' language skills in French and English were assessed at the start (Time 1) and after completion of the French learning course (Time 2). Lexical retrieval and articulation rate were assessed quantitatively from a sample of spontaneous free speech using methods similar to Berken et al. (2015) and Chai et al. (2016). Participants were asked to describe two pictures of household scenes for two minutes using the "Cookie Theft picture" from the Boston Diagnostic Aphasia Examination (Goodglass et al. 2001) and the "Divided Attention picture" from the Kentucky Aphasia Test (Marshall and Wright 2007), in English and in French, respectively. The same pictures were used for all participants in each language and at each time-point (i.e. the "Cookie Theft picture" in English at Times 1 and 2 and the "Divided Attention picture" in French at Times 1 and 2) to control for potential variations in difficulty across the pictures. The same picture was used at Time 1 and Time 2 in order to be able to use the English version as a control, as no improvement was expected in English. The total number of correct and unique words (i.e. nouns, verbs, adjectives, prepositions, and determiners) was calculated as an index of lexical retrieval (Chai et al. 2016). The mean number of syllables per second was also calculated and used as an index of articulation rate. We chose to focus on articulation rate rather than pronunciation or accent to examine articulatory aspects of language because accent has previously been linked to the basal ganglia (Berken et al. 2016). Both measures were extracted in French and English at Time 1 and Time 2, and the difference

between the two time points was used as a measure of improvement in lexical retrieval and articulation rate.

Imaging acquisition

Imaging data were acquired on a Siemens 3 Tesla MAGNETOM Prisma scanner at the McConnell Brain Imaging Centre at the MNI. Diffusion-weighted MRI data were acquired using a multi-band EPI sequence (TR=3000 ms; TE=71.0 ms; 81 slices; b-values = 300, 1000, 2000 s/mm²; 108 gradient directions; voxel size= 2mm³). High-resolution T1-weighted images were acquired using an MPRAGE sequence (TR=2300 ms; TE=2.96 ms; flip angle =9°; 192 slices; voxel size= 1 mm³). Images were acquired at Time 1 and Time 2, but given the focus of this study on neuroanatomical predictors of language learning, only the Time 1 results are of relevance here.

Imaging analysis

TractoFlow and processing

Both the T1 and diffusion-weighted images were pre-processed using the TractoFlow pipeline (Di Tommaso et al. 2017; Kurtzer et al. 2017; Theaud et al. 2020).

Diffusion-weighted images

The pipeline includes 14 steps for diffusion-weighted image (DWI) processing and extracts both diffusion tensor imaging (DTI) metrics and fibre orientation distribution function (fODF) metrics. The main steps included denoising using the *dwidenoise* tool from MRtrix3 (Tournier et al. 2019), correction of deformation induced by the magnetic field susceptibility artefacts and eddy-currents as well as brain extraction using the FSL package (Smith 2002; Jenkinson et al. 2012), N4 bias correction, cropping, normalisation and resampling before extracting the DTI and fODF

metrics was applied (Garyfallidis et al. 2014). The number of shells specified to compute the DTI metrics were "0 1000", and "0 1000 2000" for the fODF shells.

T1-weighted images

The processing for the T1-weighted images in the pipeline consists of 8 steps, including denoising (Garyfallidis et al. 2014), N4 bias correction and brain mask extraction (Avants et al. 2008), registration of the T1 image to the DWI space (Avants et al. 2008) and tissue segmentation (Jenkinson et al. 2012) to compute the tracking maps.

Tractography

Whole-brain tractograms were generated using anatomically-constrained particle-filtering probabilistic tractography (Girard et al. 2014; Barbeau et al. 2020; Theaud et al. 2020) and seeding from the white matter/grey matter interface with 10 seeds per voxel and other parameters left as default. Finally, streamlines that were found to make a 300-degree loop onto themselves were removed (Barbeau et al. 2020).

SLF II and SLF III Tract dissections

In order to implement the dissection protocol proposed by Barbeau et al. (2020), we first transformed the whole-brain tractograms into MNI space by using SyN ANTS (Avants et al. 2008) between the T1 image and the MNI 152 symmetric template and applying the transformation to the tractogram (Greene et al. 2018). Tract reconstructions were carried out manually using Trackvis (Wang et al. 2007) by creating Regions of Interest (ROIs) overlaid on individual normalised anatomical images in order to locate accurately the gyri and sulci for each participant, using coordinates and landmarks from Barbeau et al (2020).

A first common inclusion ROI was created in the frontal lobe containing pars triangularis (area 45), pars opercularis (area 44), ventral premotor area 6 that controls the orofacial musculature and areas 8a and 9/46 (single sphere, 30 mm radius centred at MNI coordinates x = -53, y = 27, z = 20 for the left hemisphere and at x = 49, y = 27, z = 20 for the left hemisphere and at x = 49, y = 27, z = 20 for the right hemisphere). For SLF II, a second inclusion ROI was created in the AG (sphere, 20 mm radius centred at MNI x = -41, y = -68, z = 38 in the left hemisphere and x = 41, y = -65, z = 38 in the right hemisphere). The "either end" option was selected for both those ROIs to include fibres originating and terminating within those regions. Another inclusion ROI was drawn in the coronal view of the FA-colour map, immediately under the central sulcus, to capture only fibres that are part of the frontoparietal white matter.

For SLF III, an inclusion ROI was created in the SMG (sphere, 20 mm radius centred at MNI coordinates x = -55, y = -42, z = 36 for the left hemisphere and x = 55, y = -39, z = 37 for the right hemisphere), with the lower end of the sphere placed at the descending posterior ramus of the lateral fissure which separates the posterior end of the temporal lobe from the adjacent SMG of the parietal cortex. This approach ensured that no fibres originating in the nearby posterior temporal gyrus were included. The AG sphere used for the reconstruction of SLF II was an exclusion ROI for SLF III so that only fibres originating from the SMG were included.

Following Barbeau and colleagues (2020), the size of the spheres used was determined based on the size of the target area to ensure all the WM was included, focusing on distinguishing connectivity within the inferior parietal lobule.

To account for the individual variability that remains after normalisation to MNI space, especially in the IPL, the SMG and AG ROI spheres had to be adjusted to fit individual anatomical landmarks (sulci and gyri). In addition, remaining streamlines clearly not belonging to the tracts of interest were removed with additional exclusion ROIs on a case-by-case basis. After the tract dissections were completed, we extracted a measure of WM integrity, Fractional Anisotropy (FA), for SLF II and SLF III in both hemispheres for all participants, i.e. an MRI measure of the diffusion of water molecules in the brain. If their diffusion is constrained by obstacles, such as myelinated WM fibres, it is expected to be anisotropic. We chose to focus on FA because of its widespread use as an index of WM microstructure, as well as the previous links between FA values and L2 learning success (Wong et al. 2011; Qi et al. 2015).

Statistical methods

Paired t-tests were conducted to compare performance across Time 1 and Time 2 for each behavioural measure. We tested the hypothesised relationships between WM integrity (FA values) of SLF II and SLF III at Time 1 and behavioural improvement (Time 2 - Time 1) using directed Pearson correlations based on specific hypotheses. Specifically, we tested the SLF II FA values in relation to L2 improvement in lexical retrieval, and SLF III FA values in relation to improvement in L2 articulation rate. Differences in correlation coefficients between groups were tested using Fisher r-to-z transformations.

<u>Results</u>

Behavioural results

As expected, participants showed no difference in English across timepoints for lexical retrieval $(t_{(17)}=0.21, p=0.8)$ or articulation rate $(t_{(17)}=0.39, p=0.7, as shown in$ **Table 2**). However, participants improved significantly on the trained language, French, between Time 1 and Time 2 for both behavioural measures of interest (**Table 2**). For L2 (French), lexical retrieval scores (number of correct unique words) increased significantly $(t_{(17)}=5.9, p<0.0001)$ between Time 1

and Time 2. Articulation rate (syllables per second) also increased significantly ($t_{(17)}$ =4.2, p<0.001) at Time 2 compared to Time 1.

<Table 2>

Tract dissections

Both the SLF II and SLF III were successfully reconstructed in both hemispheres for all participants (see **Figure 1**). Dissections were considered successful when the fibres coursed towards the frontal lobe originating specifically from the AG for SLF II, and from the SMG for SLF III, with SLF II coursing more medially and SLF III more laterally, as per Barbeau et al. (2020) and tracer studies in monkeys (Petrides and Pandya 1984). Measures of WM integrity were extracted for SLF II (left mean FA = 0.392 ± 0.03 , right mean FA = $0.405 \pm .029$, **Table 3**) and for SLF III (left mean FA = 0.415 ± 0.029 , right mean FA = 0.4124 ± 0.025 , **Table 3**), as well as for the whole brain (mean whole brain FA = 0.398 ± 0.018). There was substantial variability in lateralisation between participants. For SLF II, six participants had greater FA in the left hemisphere.

<Table 3>

Time 1 SLF II FA and vocabulary change after learning

To investigate the hypothesis that SLF II is involved in lexical retrieval, we conducted correlation analyses between the FA values for SLF II and lexical retrieval improvement based on training. We were specifically interested in how SLF II WM integrity in the left hemisphere related to lexical retrieval improvement after learning. FA values of the left SLF II at Time 1 correlated positively with improvement in lexical retrieval (Time 2 - Time 1) in French (see **Figure 2.a**, r = 0.545, p = 0.019), which indicates that individuals with higher initial FA improved more in the

number of unique words produced after French training. FA of the right SLF II was not correlated with improvement in lexical retrieval (r=0.023, p=0.9). Furthermore, articulation rate was not correlated with FA in this tract in either hemisphere (r=0.229, p=0.3 for the left and r = 0.157, p = 0.5 for the right), suggesting that the link between the initial FA of SLF II and behavioural change is specific to the left hemisphere and related to lexical retrieval improvement. In addition, Fisher r-to-z transformation showed that the correlation coefficients between the English L1 and Mandarin L1 groups did not differ (z= -0.36, p=0.7) and between the male and female participants did not differ either (z=1.41, p=0.15), and whole brain FA did not predict improvement in lexical retrieval (r= 0.240, p=0.3).

Time 1 SLF III FA and articulation rate change after learning

To investigate the hypothesis that SLF III is involved in articulation, we conducted correlation analyses between the FA values for SLF III at Time 1 and improvement in articulation rate after training. We were specifically interested in how SLF III WM properties in the left hemisphere related to change in articulation rate. Left SLF III FA values at Time 1 were positively correlated with improvement in articulation rate (Time 2 - Time 1) (see **Figure 2.b**, r= 0.583, p=0.011), which indicates that participants who had a higher initial FA showed more improvement in articulation rate after learning. FA of the right SLF III was not correlated with change in articulation rate (r=0.219, p=0.3). Lexical retrieval change was not correlated with FA of this tract in either hemisphere (r=0.337, p=0.1 for the left and r=0.077, p=0.7). This indicates the link between the initial WM properties of SLF III and behavioural improvement is specific to the left hemisphere and to articulation rate improvement. In addition, Fisher r-to-z transformation showed the correlation coefficients between the English L1 and Mandarin L1 groups did not differ (z=0.12, p=0.9) and between the male and female participants did not differ either (z=0.12, p=0.9), and whole brain FA did not predict improvement in articulation rate (r= 0.367, p=0.1).

Discussion

The aim of this study was to examine the specific roles of SLF II and SLF III in second language (L2) learning by using precise anatomical tractography to examine their respective functional contributions to L2 learning success. We examined intrinsic structural connectivity from the IPL (SMG and AG) to the frontal language regions via the SLF II and SLF III pathways to establish anatomical predictors of L2 learning success following language training. A dissociable pattern of correlations between WM integrity measures of the two pathways and their hypothesised involvement in language was observed. Pre-training left SLF II FA predicted improvement in lexical retrieval specifically, while pre-training left SLF III FA was only related to improvement in articulation rate. Thus, as a result of the anatomical separation of the SLF II and III, we provide empirical support for the hypothesised respective roles of these two separate branches of the left SLF in L2 learning.

The issue of separating the SLF II and III was of particular importance for this study in the context of L2 learning, as the IPL has been shown to be involved in L2 acquisition. Thus, the anatomical projections of the IPL to the language areas of the ventrolateral prefrontal cortex are relevant. Several studies have shown that the IPL is a critical brain region for various aspects of L2 proficiency and learning. Mechelli et al. (2004) reported that GM density was higher in the left IPL of more proficient bilinguals. Increased GM density of the IPL has also been observed in multilingual individuals (Grogan et al. 2012), in bilinguals with higher measures of multilingual competence (Della Rosa et al. 2013), and in studies of speech imitation aptitude (Reiterer et al. 2011). Furthermore, higher WM density of the IPL has been related to better pronunciation of foreign sounds (Golestani and Pallier 2007). Increased activation of the left IPL in fMRI studies has also been associated with L2 learning in relation to reading speed (Barbeau et al. 2017) and

tone discrimination (Yang et al. 2015). In terms of frontoparietal connectivity and L2 learning, Yang et al. (2015) reported that better communication between the IPL and frontal cortex leads to more successful lexical processing of the tonal information in novel words in Mandarin. Connections between frontal and parietal areas have also been shown to relate to language analytical abilities, a component of language aptitude (Kepinska et al. 2017). In addition, subnetworks of WM connecting frontal areas to the IPL (SMG and AG) have been found to be more strongly connected in bilinguals than monolinguals (García-Pentón et al. 2014). Thus, the role of the IPL in L2 learning and individual aptitude is well supported, as well as the importance of a frontoparietal network of connectivity.

One of the strengths of the present study is the use of a priori anatomical knowledge to define SLF II and SLF III using diffusion MRI tractography (Barbeau et al. 2020). Inconsistent definitions of pathways have been particularly problematic in the context of language research (see Dick and Tremblay 2012 for review). Here, we based our definitions of SLF II and III on autoradiographic tracer studies, which are considered the gold standard for establishing anatomical connectivity in the brain, because they allow the establishment of the precise origin, trajectory, and termination of axons. In addition, knowledge of these WM tracts coming from macaque tracer studies is supported by evidence of corresponding resting-state functional connectivity in the human brain (Kelly et al. 2010; Margulies and Petrides 2013; Jakobsen et al. 2016). Comparable parallels between human and monkey brains have been drawn in relation to the mirror neuron system, which is found in the monkey homologue of area 44 and human area 44, and has been linked to speech processing (Rizzolatti and Arbib 1998; Corballis 2010); such studies support the relevance of non-human primate models to further our understanding of the anatomy of language in the human brain.

Using improved reconstructions of pathways, we examined the roles of the SMG (area 40) and the AG (area 39) and their respective frontal connections in order to disentangle their possible functional contributions. In particular, we were able to demonstrate a relationship between the FA values in SLF II and improvement in lexical retrieval (i.e. the number of new correct and unique words produced) during second language learning, consistent with the hypothesised role of this tract in language processing. Indeed, area 45 has been shown to be involved in the controlled selective retrieval of information (Petrides 2002), notably in the left hemisphere for verbal information (Klein et al. 1995; Petrides et al. 1995; Heim et al. 2009), while area 8a is involved in regulating attention (Petersen and Posner 2012; Petrides 2015). Several studies have highlighted the involvement of the AG in aspects of verbal retrieval (Price 2010; Seghier 2012; Herbet et al. 2016; Linden et al. 2017), as well as semantic processing (Binder et al. 2009; Van Ettinger-Veenstra et al. 2016). Moreover, the few studies referring to SLF II in the context of language appear to support the role of this tract in retrieval of verbal and semantic information (Madhavan et al. 2014; Akinina et al. 2019; Nakajima et al. 2020). Taken together, our finding that SLF II structure is predictive of the ability to retrieve new L2 vocabulary is consistent with previous research and suggests a potential role for the SLF II in facilitating improvements in L2 lexical learning.

Similarly, the association between the FA of SLF III and improvement in articulation rate is consistent with the literature (Kellmeyer et al. 2013; Duffau et al. 2014; Nakajima et al. 2020). The orofacial portion of area 6 in the ventrolateral precentral gyrus is essential for articulation (Bouchard et al. 2013). Area 44 has been proposed as an intermediary area between cognitive retrieval and articulation (Petrides 2014), given its position between area 45 and the ventral premotor system, and has been shown to be involved in various aspects of speech production, such as phonological processing (Heim et al. 2008; Heim et al. 2009; Church et al. 2011; Clos et al. 2013), articulatory planning (Papoutsi et al. 2009; Price 2010) and other motor aspects of

language (Horwitz et al. 2003; Nakajima et al. 2020). Area 9/46v is involved in working memory and enabling high-level planning and behavioural organisation (Petrides 2015). There is also evidence that the SMG is involved in phonological processing (Oberhuber et al. 2016) and speech output (Price 2010; Oberhuber et al. 2016), particularly when speech production is made more difficult, which could include production in a second language, as well as selecting phonological information for language production (Corina et al. 1999). By connecting relevant brain regions, SLF III could enable speech production by facilitating the retrieval of phonological information and establishing motor articulatory plans (Rodríguez-Fornells et al. 2009); thus, better integrity of the SLF III tract could promote improvement in speed of speech output, consistent with what has been shown in the present study.

Interestingly, we did not find any group differences between the English monolingual and the Mandarin-English bilingual participants, which could indicate that these predictors of L2 success are present in individuals regardless of language background. However, in order to draw broader conclusions, the current results need replication with a larger sample and particularly in a sample undergoing longer-term language training, as well as in participants with other language backgrounds.

Conclusion

Examining structural connectivity is crucial to understanding the functions of a given brain region, because knowing the other brain areas it specifically and directly interacts with informs us about the roles of the region of interest. Thus, being anatomically precise when examining white matter (WM) connections is relevant for elucidating functional differentiation between brain regions. In the present study, we report that the properties of the left SLF II support learning

novel vocabulary in an L2, while the left SLF III supports articulation rate in the L2. This functional dissociation is in line with the previously suggested roles for SLF II and SLF III in language (Nakajima et al. 2020). Anatomical separation of SLF II and SLF III with tractography has rarely been demonstrated, and functional dissociation of these tracts in language learning had not been demonstrated before. The anatomical tract dissections in the present study allowed higher specificity in examining the functional contributions of the SLF II and SLF III and enabled us to demonstrate a functional dissociation between these branches of the SLF. In addition, these findings suggest that individual differences in L2 learning abilities can be explained by variations in intrinsic anatomical connectivity between specific language regions of the brain. Overall, the results reported here add to our understanding of the language networks that support L2 learning and its neuroanatomical predictors.

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<u>Tables</u>

| | English L1 | Mandarin L1 | t statistic | p value |
|-------------------------------|-------------|--------------|-------------|---------|
| Digit Span: Forward (/16) | 11.7 ± 1.70 | 10.25 ± 1.91 | 1.70 | 0.108 |
| Digit Span: Backward (/16) | 8.6 ± 2.01 | 9.4 ± 2.07 | 0.83 | 0.420 |
| Digit Span: Sequencing (/16) | 8.3 ± 1.06 | 8.1 ± 2.30 | 0.25 | 0.809 |
| Letter-Number Sequencing (/30 | 20.1 ± 1.3 | 19.8 ± 1.3 | 0.49 | 0.633 |
| Matrix Reasoning (/26) | 22.5 ± 1.12 | 22 ± 1.58 | 0.79 | 0.443 |

Table 1. Mean ± SD of the WAIS-IV scores on various subtests for the English and Mandarin groups.

 Table 2. Mean ± SD (range) of the number of correct words produced (lexical retrieval) and syllables per second (articulation rate) before (Time 1) and after (Time 2) learning.

| Lexical retrieval | | Articulation rate | | |
|-------------------|----------------------|-------------------------|-------------------------|--|
| French | English | French | English | |
| 30.5 ± 11 (18-55) | 106.61 ± 45 (39-208) | 0.76 ± 0.2 (0.54-1.32) | 2.73 ± 0.64 (1.87-4.01) | |
| 45.0 ± 11 (28-66) | 105.72 ± 39 (45-164) | 0.92 ± 0.22 (0.58-1.27) | 2.70 ± 0.64 (1.56-2.84) | |

Table 3. Mean ± SD of FA for SLF II and SLF III in the left and right hemispheres

| Left FA | Right FA |
|---------------|----------------|
| 0.392 ± 0.03 | 0.405 ± .029 |
| 0.415 ± 0.029 | 0.4124 ± 0.025 |

Captions to figures

Figure 1. Example of the SLF II (red) and the SLF III (yellow) dissections in one participant. **a)** Left hemisphere. **b)** Right hemisphere. **c)** Illustrations of the frontal (orange), supramarginal (SMG, yellow) and angular (AG, red) ROI spheres in two different sagittal sections. SMG and AG appear to overlap but are either inclusion or exclusion ROIs depending on the tract of interest. ROIs appear to extend beyond the brain to ensure fibres terminating in the white matter are included, but no fibres are present outside the brain and therefore, not included.

Figure 2. Relationship between behavioural improvement and pre-learning FA values of the left hemisphere. **a**) Improvement in lexical retrieval (number of words) plotted against the left SLF II FA. **b**) Improvement in articulation rate (syllables/second) plotted against the left SLF III FA.





