Interhemispheric Functional Brain Connectivity Predicts New Language Learning Success in Adults

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Running title: Interhemispheric connectivity and L2 learning success

ABSTRACT

Investigating interhemispheric interactions between homologous cortical regions during language processing is of interest. Despite prevalent left hemisphere lateralisation of language, the right hemisphere also plays an important role and interhemispheric connectivity is influenced by language experience and is implicated in second language (L2) acquisition. Regions involved in language processing have differential connectivity to other cortical regions and to each other, and play specific roles in language. We examined the interhemispheric interactions of subregions of the inferior frontal gyrus (areas 44 and 45), the adjacent area 9/46v in the middle frontal gyrus, the superior temporal gyrus (STG) and the posterior inferior parietal lobule (pIPL) in relation to distinct and specific aspects of L2 learning success. The results indicated that the connectivity between left and right areas 44 and 9/46v predicted improvement in sentence repetition, connectivity between left and right area 45 and mid-STG predicted improvement in auditory comprehension and connectivity between left and right pIPL predicted improvement in reading speed. We show interhemispheric interactions in the specific context of facilitating performance in adult L2 acquisition that follow an anterior to posterior gradient in the brain, and are consistent with the respective roles of these regions in language processing.

Keywords: individual differences; neural biomarkers; resting-state functional connectivity; second language

The notion of involvement of bilateral brain networks in language processing is becoming more established in the literature. Although leftward asymmetric lateralisation of language in most of the population is well established (Geschwind 1970; Geschwind & Galaburda 1985; Friederici 2011), the extent of participation of each cerebral hemisphere depends on the nature of the task (Chang & Lambon Ralph, 2020). An increasing body of research is identifying the role that the right hemisphere (RH) plays in language (Vigneau et al. 2011; Van Ettinger-Veenstra et al. 2012), especially in the context of second language (L2) learning (see Qi & Legault 2020 for review). In particular, it is currently thought that the RH is involved in the early stages of L2 learning (Qi et al. 2015; Xiang et al. 2015; Kepinska et al. 2018), when proficiency is lower (Reiterer et al. 2009; Sebastian et al. 2011). Although much research has been carried out to characterise the contributions of each cerebral hemisphere to language, it is less well understood how the two hemispheres communicate with each other to achieve complex cognitive operations. It is, therefore, of interest to understand how the two hemispheres communicate and cooperate in the context of language processing and L2 learning (Perrone-Bertolotti et al. 2013a).

Examining how various brain regions function together to enable specific cognitive processing is of importance in developing a comprehensive model of language organisation in the brain. The use of functional Magnetic Resonance Imaging (fMRI) allows us to examine functional connectivity (FC) between cortical areas by looking at the temporal correlation between the blood-oxygen-level-dependent (BOLD) signals of specific voxels in brain regions. It is known that there is strong functional connectivity between homologous regions of the two hemispheres

(Stark et al. 2008; Roland et al. 2017), which is partly preserved even in individuals in whom there is an absence of the corpus callosum (CC), indicating that homologous regions also communicate via indirect pathways (Tyszka et al. 2011; Siffredi et al. 2021). Thus, interhemispheric connectivity refers to regions between the hemispheres that function together, whether this interaction is mediated by direct anatomical connections or not. There are competing theories regarding whether the interhemispheric interactions are inhibitory (one hemisphere inhibiting the other when performing a task) or excitatory (information being transferred and integrated between the hemispheres to perform certain tasks), with some agreeing that both may be true depending on the processing demands of the task being carried out (see van der Knaap & van der Ham 2011; Kasselimis & Nidos 2015, for review). In terms of functional outcomes of interactions between the hemispheres, it has been established for some time that interhemispheric interaction can facilitate performance, particularly during demanding tasks (Banich 1998; Scalf et al. 2009; Höller-Wallscheid et al. 2017). Indeed, transferring information between the hemispheres, and thus bilateral neural recruitment, may be advantageous to perform complex cognitive tasks (Kasselimis & Nidos 2015). Thus, interhemispheric connectivity, as measured by fMRI, may represent the degree of communication and integration between the hemispheres required for specific functions (Jin et al. 2020). In the context of the language network, evidence shows that interhemispheric interactions occur and are beneficial for language processing. Bilateral activations may represent evidence that information is being integrated between them (van der Knaap & van der Ham 2011; Vigneau et al. 2011).

Functional connectivity at rest (rsFC) is thought to reflect intrinsic properties of brain regions communicating and functioning together (Fox & Raichle 2007). Previous studies have linked rsFC with individual predispositions towards various skills and abilities such as motor learning (Mary et al. 2017), working memory (Fang et al. 2016; Avery et al. 2020), creativity (Cousijn et al. 2014; Bashwiner et al. 2020), learning of certain musical aspects (Hou et al. 2015; Lumaca et al. 2019), different forms of intelligence (Shearer 2020) and language learning (Wang et al. 2012; Ventura-Campos et al. 2013; Chai et al. 2016). In addition, rsFC between homologous regions in each hemisphere is thought to reflect interhemispheric functional integration (Jin et al. 2020), and measuring it could inform us about how interhemispheric functional integration can support cognitive processes, such as learning (Gee et al. 2011; Jin et al. 2020). Thus, examining the relationship between interhemispheric rsFC and L2 learning success could help elucidate whether certain individuals with stronger rsFC have an advantage in acquiring various aspects of a new language. Several studies have examined interhemispheric interaction in the specific context of facilitating performance, including language proficiency. One meta-analysis looking at the link between interhemispheric interaction and language proficiency reported that RH activation during phonological and lexico-semantic processing mainly occurred at the same time as LH activation, indicating some level of interhemispheric interaction (Vigneau et al. 2011). In addition, studies in healthy children have shown that higher interhemispheric FC is related to verbal fluency and vocabulary (Bartha-Doering et al. 2021a) and, furthermore, children with agenesis of the CC exhibit reduced interhemispheric connectivity and lower verbal abilities (Bartha-Doering et al. 2021b). There is also evidence linking bilingual experience with interhemispheric interaction, in terms of behaviour (divided visual field experiment, Ibrahim

2009), structural connectivity (Coggins III et al. 2004; Felton et al. 2017), and functional connectivity (Berken et al. 2016)**.** These studies highlight the link between the strength of interhemispheric interaction and proficiency in a second language. Structural connectivity findings indicate that the anterior mid-section of the CC is larger in bilingual individuals than monolingual individuals (Coggins III et al. 2004; Felton et al. 2017) and rsFC has been found to be stronger between the left and right inferior frontal gyrus (IFG) in bilinguals who acquired their L2 earlier (Berken et al. 2016)**.** Furthermore, a few studies have shown that interhemispheric interactions relate to L2 acquisition ability and influence the acquisition process (Veroude et al. 2010; Schlegel et al. 2012; Xiang et al. 2012; Qi et al. 2019). In terms of structural connectivity, Xiang et al. (2012) report that some aspects of language ability are mediated by interhemispheric connectivity between the left and right IFG, and Schlegel et al. (2012) found that second language learners of Chinese showed increases in Fractional Anisotropy (FA) in the genu of the CC after language training. In terms of functional connectivity, Veroude et al. (2010) reported stronger post-learning increases in FC between the supramarginal gyri in the left and right hemispheres for better learners, while Qi et al. (2019) found increases in rsFC between the left and right IFGs post-learning. Although these studies provide evidence of the importance of interhemispheric connectivity in language learning, specific investigations into the role of interhemispheric interactions in various aspects of language are still lacking, and much remains to be understood concerning the role of connectivity between specific regions.

The present study aimed to investigate the facilitative and predictive role of intrinsic interhemispheric interaction in second language learning by examining interhemispheric connectivity of several perisylvian brain regions in relation to different aspects of language. Although previous studies have reported changes in interhemispheric connectivity as a result of L2 learning (Veroude et al. 2010; Schlegel et al. 2012; Qi et al. 2019), the focus of the present investigation is on predicting L2 learning success based on the connectivity between the hemispheres. Specifically, we were interested in examining the distinct contributions of language-related regions in the inferior frontal lobe, namely area 44 in the pars opercularis and area 45 in the pars triangularis of the IFG, area 9/46v in the middle frontal gyrus (MFG), as well as the superior temporal gyrus (STG) and the posterior inferior parietal lobule (pIPL) that includes the angular gyrus (AG). These regions are of interest because of their established roles in specific aspects of language. We were particularly interested in investigating different parts of the ventrolateral frontal language region separately, as studies often treat this region as a whole (Xiang et al. 2010), despite evidence that it is composed of distinct cytoarchitectonic areas with differential contribution to language. It is known that area 44 is involved in phonological processing (Heim et al. 2009; Church et al. 2011), articulatory aspects of speech production (Heim et al. 2008; Price 2010; Clos et al. 2013) and phonological working memory (Zurowski et al. 2002), and is strongly connected to area 9/46v (see case 6 in Petrides & Pandya 2002). Areas 46 and 9/46 on the middle frontal gyrus are involved in the monitoring of information in working memory (Petrides 2002) and, given the strong connectivity of 9/46v with area 44 and the adjacent ventral premotor cortex, this specific part of the mid-dorsolateral frontal cortex may be involved in monitoring the articulatory aspects of speech in working memory. On the other hand, there is evidence that area 45 is involved in the active controlled retrieval of information from memory (Klein et al. 1995; Petrides et al. 1995; Heim et al. 2009) and certain aspects of semantic processing (Dapretto & Bookheimer 1999; Gough et al. 2005; Hagoort 2005; Mainy et al. 2007). Area 45 is connected via the Extreme Capsule Fasciculus (ECF) to the middle part of the STG (mSTG) (Petrides & Pandya 1988; Petrides 2014) that plays a role in language comprehension (Friederici 2002; Friederici et al. 2003), particularly spoken language given the involvement of the STG in auditory processing. Finally, the role of the AG in the pIPL in reading has been well established (Seghier 2012), including in relation to language comprehension (Price & Mechelli 2005; Graves et al. 2010), semantic processing (Seghier 2012) and learning to read (Carreiras et al. 2009), as well as predicting improvement in reading speed in an L2 (Barbeau et al. 2017).

We selected three distinct measures of L2 learning: 1) Repetition of orally presented sentences as reflected in the percent of words correctly repeated in terms of grammar and pronunciation. This measure involves both speech production and monitoring of the articulatory speech output in working memory and is predicted to engage areas 44 and 9/46v. 2) Listening comprehension which requires listening to a story and answering comprehension questions, thus involving auditory comprehension and retrieval of information from memory and is predicted to engage area 45 and the mSTG. Finally, 3) reading speed (Dehaene et al. 2010), reflected in the number of words per minute in a passage read aloud by participants, which requires sufficient understanding of meaning through reading, involving the pIPL. We hypothesised that intrinsic interhemispheric rsFC in each of these regions of interest (ROIs) would facilitate L2 learning and, therefore, would predict behavioural improvement related to these specific areas of language processing.

METHODS

Participants

We recruited 18 participants (mean age 20.8 years ± 3.9, range 17-32, 12 females) from a French language-learning course. The course was a university-level course for beginners offered by the McGill French Language Centre, consisting of approximately 80 h of training over one or two semesters, focusing on grammar, writing, comprehension, and discussion of both audio passages and written documents to provide comprehensive training. The inclusion criteria for the study were right-handedness, normal or corrected-to-normal vision, no reported hearing impairments, no history of traumatic brain injury, neurological disorders, or conditions incompatible with MRI scanning, as well as having no advanced musical training, because of the known link between musical training and language ability (see Milovanov & Tervaniemi 2011 and Jäncke 2012 for review). Advanced musical training was defined as being a professional or expert musician; participants who did have musical training received it in primary or high school, and of those, none still regularly played at the time of testing. At the time of the study, all participants were McGill University students, studying in English, and were beginner French learners. The participants included two subgroups whose native (L1) languages were American English (n=10) or Mandarin (n=8) with English being the second language (L2). These participants were selected because they were the largest, most homogeneous groups of eligible participants. Proficiency in a language other than English or Mandarin was an exclusion criterion. No group differences were found in working memory and general intelligence, measured by the Digit Span, Letter-Number Sequencing, and Matrix Reasoning subtests of the WAIS-IV (Wechsler Adult Intelligence Scale; Wechsler 2008), or in behavioural improvement or rsFC (see Table 1) and, therefore, participants were treated as a single group for all analyses. The present study was approved by the Research Ethics Board of the Montreal Neurological Institute (MNI) and the participants gave informed written consent.

Language tasks

Language abilities were assessed at two time points, pre- (time 1) and post- (time 2) language training, i.e. prior to and after completion of the French language course, in both English (control language) and French (trained language). The sentence repetition task was the Recalling Sentences subtest of the Clinical Evaluation of Language Fundamentals (4th edition) (Semel et al. 2003). The examiner read 24 sentences aloud, one at a time, to the participants, who repeated each one immediately after hearing it. The responses were recorded and then transcribed in order to calculate the percentage of words correctly repeated (i.e. pronounced comprehensibly and in the correct order in the sentence); the average of all 24 sentences was taken as the sentence repetition score. The transcription was scored by a native Quebec French speaker for accuracy of reproduction, and the scoring was then verified by a second native French speaker with overlap in agreement between raters. The listening comprehension task consisted of auditory presentation of a story followed by 17 comprehension questions about the story (Story Learning and Memory test, adapted versions in English and French from tests in use at the Montreal Neurological Institute (MNI), Wechsler 1987). Participants' responses were recorded, and a score was calculated as the percentage of questions answered correctly (content). The reading speed score was the number of words read per minute from another passage also taken from the same Story Learning and Memory test. Each measure was calculated from French and English versions of the tests at time 1 and time 2, and the difference between the two time points was used as a measure of improvement for each language.

Imaging

Acquisition

Imaging data were acquired before the start of the French course (time 1) on a Siemens 3 Tesla MAGNETOM Prisma scanner at the McConnell Brain Imaging Centre of the MNI. Resting-state fMRI data were acquired using multi-band echo-planar imaging (EPI) (acceleration factor = 6, TR=930ms, TE=30ms, 72 slices 2 mm thick, voxel size= 2 mm^3) for 10 minutes while participants focused on a fixation cross on the screen. High-resolution T1-weighted images were obtained using a magnetisation prepared rapid acquisition gradient echo (MPRAGE) sequence (TR = 2300 ms; TE = 2.96 ms; flip angle = 9°; 192 slices; voxel size = 1 mm^3).

Analysis

The resting-state fMRI data were preprocessed using SPM12 (Wellcome Department of Imaging Neuroscience, London, UK) using standard preprocessing steps. Images underwent realignment and unwarping, normalising in MNI space, and smoothing with a 6mm kernel. Motion outlier images were detected using ART (Artifact Detection Tools) and defined as images that deviated by more than 3 SDs from the mean image intensity of the session or having composite head movement exceeding 1 mm from the previous image (Whitfield-Gabrieli & Nieto-Castanon 2012; Nieto-Castanon 2020). Denoising of the fMRI time series and functional connectivity analysis were performed using the CONN toolbox (Whitfield-Gabrieli and Nieto-Castanon 2012). Anatomical CompCor method (aCompCor, Behzadi et al. 2007) was applied to reduce physiological noise in the resting-state data. Specifically, five principal components of the eroded masks of white matter and CSF were included as regressors in the general linear model to achieve optimal noise reduction (Chai et al., 2012). A temporal bandpass filter of 0.008-0.09 Hz was applied to the time series. Regressors for outlier timepoints and head motion parameters were included in the general linear model to account for motion-related artifacts. An ROI-to-ROI functional connectivity analysis was carried out to examine specific functional connectivity between the regions of interest and their RH homologues, i.e. the temporal correlations between the blood oxygen level-dependent (BOLD) signal in a chosen ROI and that in other target ROIs were computed. Functional connectivity values (Fisher's Z scores of the Pearson's correlation coefficient) between the selected ROIs and their targets were extracted for each participant.

ROIs

The ROIs were selected based on a priori knowledge of cytoarchitecture and anatomical connectivity in the ventrolateral frontal cortex (Petrides et al. 2012; Petrides 2014), the superior temporal gyrus (Petrides and Pandya 1988; Petrides and Pandya 2009; Petrides 2014) and inferior parietal lobule (Petrides and Pandya 2009; Petrides 2014). We used parcellations of the IFG pars triangularis (area 45) and pars opercularis (area 44) from the Harvard-Oxford atlas that is implemented in the Conn toolbox (Whitfield-Gabrieli and Nieto-Castanon 2012). Given that this atlas has only a parcellation for the whole MFG, and that 9/46v is a specific part of the MFG, we created a smaller ROI in order to look at its functional connectivity. This ROI was defined by the inferior frontal sulcus ventrally, the anterior segment of the posterior middle frontal sulcus anteriorly and the intermediate segment of the posterior middle frontal sulcus posteriorly (Petrides 2019). In addition, the Harvard-Oxford atlas only has parcellations for the anterior and posterior STG and therefore we created one for the middle STG. The middle STG region included the superior temporal sulcus (STS), using Heschl's gyrus as the posterior limit. We also created a specific ROI in the posterior part of the inferior parietal lobule (pIPL), extending from the posterior border of the supramarginal gyrus to the angular gyrus as far as the angular sulcus (caudal superior temporal sulcus 2nd ramus, ans/csts2) (Petrides 2019), mostly encompassing the AG as well as the most posterior border of the SMG. The area 9/46v, mSTG and AG ROIs were hand-drawn within the previously defined limits using the ROI tool in MRView (Tournier et al. 2019). The ROIs are shown in Figure 1, and their MNI coordinates (centre of gravity) and volumes can be found in Table 2. Since the interhemispheric connectivity of the different regions was compared to behavioural improvement and not directly to each other, the minor differences in volume (which can vary even within an atlas) are not considered to affect the interpretation of the results. Additional ROIs were created as 6mm spheres for the left (centre coordinates: -36 -22 56) and right (centre coordinates: 36 -20 58) hand motor regions as non-language ROIs to serve as control areas.

Statistical methods

Paired t-tests were conducted to compare performance from time 1 to time 2 for each behavioural measure. We tested the hypothesised relationships between interhemispheric rsFC at time 1 and behavioural improvement (time 2–time 1) using Pearson correlations based on our specific hypotheses. Specifically, we tested the area 45 and mSTG interhemispheric rsFC values in relation to L2 improvement in listening comprehension, area 44 and 9/46v values in relation to improvement in L2 sentence repetition and pIPL interhemispheric FC in relation to improvement in L2 reading speed. The reported p-values for correlations of the hypothesised rsFC-behavioural improvement relationships of interest are corrected for multiple comparisons (FDR). Assumptions of level of measurement, linearity, normality and related pairs were met. Non-parametric testing using the bootstrap method (resampling with replacement with 1000 iterations) was also used to confirm findings, as implemented by the boot function (Davison & Hinkley 1997; Canty & Ripley 2021) in R (R Core Team 2020). Differences in correlation coefficients between male and female participants were tested because of some reports of sex differences in language lateralisation (Bitan et al. 2010; Scheuringer et al. 2020), using Fisher r-to-z transformations.

RESULTS

Behavioural results

As expected, there was no improvement in the control language, English, between time 1 and time 2 on any of the behavioural measures (Table 3). However, there was significant improvement in the language of training, French, after learning, for all three measures, as shown in Table 3.

* It should be noted that, at the individual level, one participant has a negative improvement score for sentence repetition improvement, and another for reading speed. It seems unlikely that the performance of these individuals decreased after language learning, and rather means that their improvement after the course was minimal and their performance on the day of testing happened to be worse. We chose to include all our participants in the analysis as they represent the full range of learning performance.

Pre-learning interhemispheric connectivity predicts language improvement

Areas 44 and 9/46v in relation to sentence repetition

There were positive correlations specifically between the interhemispheric rsFC of area 44 and of area 9/46v with improvement in sentence repetition in French (r=0.48, p=0.043 and r=0.52, p=0.05, respectively; see Figure 2). Thus, individuals with higher rsFC between left and right areas 44 and left and right areas 9/46v showed greater improvement in the ability to repeat sentences in French correctly immediately after hearing them. Importantly, these relationships were specific to sentence repetition improvement. Comprehension improvement was not significantly related to interhemispheric connectivity of either area 44 (r=0.15, p=0.551) or area 9/46v (r=0.19, p=0.447). Likewise, reading speed improvement was not significantly related to interhemispheric connectivity of either area 44 (r= 0.28, p=0.261) or area 9/46v (r=0.25, *p*=0.313). There were no differences between male and female participants (*z*=0.7, *p*=0.48 and *z*=1.37, *p*=0.17, respectively).

Area 45 and mSTG in relation to listening comprehension

There were specific positive correlations between area 45 and mSTG interhemispheric rsFC and improvement in listening comprehension in French (*r*=0.55, *p*=0.018 and *r*=0.57, *p*=0.026, respectively; see Figure 3). Individuals with higher pre-learning rsFC between the left and right area 45, as well as between the left and right mSTG, demonstrated greater improvement, as indicated by the higher percentage of questions that were correctly answered after listening to a story in French. Critically, these correlations were specific to improvement in listening comprehension. Sentence repetition was not related to interhemispheric connectivity of area 45 (*r*=0.33, *p*=0.176) or mSTG (*r*=0.34, *p*=0.172). Nor was reading speed related to interhemispheric connectivity of area 45 (*r*=0.39, *p*=0.109) or mSTG (*r*=0.2, *p*=0.433). There were no differences between male and female participants (*z*=0.84, *p*=0.4 for area 45 and *z*=-1.2, *p*=0.23 for mSTG).

Posterior inferior parietal lobule (pIPL) and reading speed

The interhemispheric rsFC of the pIPL pre-learning was significantly and specifically correlated with improvement in reading speed (*r*=0.5, *p*=0.041; see Figure 4). Individuals with higher rsFC between the angular gyri of left and right hemispheres improved more in the number of words read per minute while reading a passage aloud. This result was specific to improvement in reading speed (r=0.37, p=0.126 for sentence repetition and r=0.45, p=0.06 for comprehension). There were no differences between male and female participants (z=0.67, p=0.50).

Additional results

Non-parametric testing using bootstrapping corroborates the above reported findings. All hypothesized brain connectivity-behavior relationships reported above were significant (ps < 0.05). The distribution of correlation coefficients from the bootstrap procedure yielded a single peak for all hypothesised connectivity-behavior relationships, which suggests that the correlations do not appear to be driven by outliers (Singh & Xie 2003). Analyses using the interhemispheric rsFC of the control hand motor regions showed no significant correlations with any of the behavioural improvement measures (sentence repetition: r=0.08, listening comprehension: r=-0.012 and reading speed: r=0.04). In addition, no significant relationships were found between pre-learning interhemispheric rsFC and pre-learning language abilities (area 44 - sentence repetition: r=-0.27, area 9/46v - sentence repetition: r=0.1, area 45 - listening comprehension: r=-0.22, mSTG - listening comprehension: r=0.35 and AG - reading speed: r=-0.041).

DISCUSSION

Although functional hemispheric asymmetries have long been demonstrated to be important for different aspects of cognitive processing (Gazzaniga 2000), there is increasing evidence for how the two cerebral hemispheres work together. In the context of language processing, few studies have provided direct examinations of the role of interhemispheric communication and connectivity in learning a new language. The results from the present study suggest that greater interhemispheric connectivity pre-learning predicts learning success of a new language in adults and that this connectivity is predictive of success in specific aspects of language learning. The location in terms of the connectivity between language-related areas follows an anterior to posterior pattern, in line with the predicted functional roles of cortical areas in language. Individuals with higher rsFC between the left and right areas 44 and left and right 9/46v improved more in sentence repetition, those with higher rsFC between left and right areas 45 and left and right mSTG improved more in listening comprehension, and those with higher rsFC between left and right pIPL improved more in reading speed. Importantly, these patterns of correlation were exclusive to these ROIs and the corresponding aspects of language, and behavioural improvement was specific to the trained language, French. In addition, there were no differences between participants whose L1 was English or Mandarin, suggesting that these findings hold true regardless of language background and whether French was a second or third language. These results indicate not only that individual interhemispheric functional connectivity overall is an important factor associated with more effective learning of a new language, but that connectivity between distinct language regions in each hemisphere plays a role in promoting learning of specific aspects of the new language.

Sentence repetition has long been used to assess language abilities in various contexts (Klem et al. 2015; Andreou et al. 2021). Since we measured performance as the percent of words correctly repeated, we hypothesised that performance in this task would relate to brain regions involved in articulation, speech production and working memory. Area 44 is known 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). Of particular interest was the finding with regard to area 9/46v. The mid-dorsolateral prefrontal cortex (areas 46 and 9/46) is known to play a critical role in the monitoring of information in working memory (Petrides 2000) and, therefore, it was of interest that the ventral part of this region, area 9/46v which is strongly connected with area 44 and the ventral part of the premotor cortex that controls the orofacial musculature (Petrides 2015), was here shown to be involved in the monitoring of the articulatory aspects of speech in working memory**.** Thus, better communication between left and right areas 44 and 9/46v could support improvements in working memory and speech production in a new language, which is consistent with the literature and the present findings.

The listening comprehension task required auditory comprehension and retrieval of relevant information. Listening comprehension is known to elicit bilateral activations (Jung-Beeman 2005; Price 2010; Friederici 2011; Vigneau et al. 2011) and to involve the ventral stream of language processing (Hickok & Poeppel 2004; Saur et al. 2008) that is mediated by the temporo-frontal extreme capsule fasciculus connecting area 45 to the mSTG (Petrides & Pandya 1988; Petrides & Pandya 2009). Area 45 is involved in active controlled retrieval of information from memory (Klein et al. 1995; Petrides et al. 1995; Petrides 2002; Petrides 2006; Heim et al. 2009) and in semantic processing and comprehension (Dapretto & Bookheimer 1999; Gough et al. 2005; Hagoort 2005; Mainy et al. 2007). The STG has a well-established role in auditory processing and comprehension (Friederici et al. 2000; Friederici 2002; Friederici et al. 2003; Gernsbacher & Kaschak 2003). In addition, there is evidence that FC between the left and right pSTG predicts better receptive language performance in people recovering from brain injury (Dick et al. 2013) and that interhemispheric interactions are important for speech comprehension (Friederici et al. 2007). Thus, stronger interhemispheric rsFC facilitating interactions bilaterally between areas 45 and the mSTG could contribute to improvement in speech comprehension and retrieval from memory.

Finally, the role of the inferior parietal lobule in reading, particularly the AG, is well established (Horwitz et al. 1998; Seghier 2012). Alexia, which affects the ability to read out loud, is commonly associated with lesions of the left AG (Henderson 2014). There is also evidence linking the AG with semantic aspects of reading (Price & Mechelli 2005; Graves et al. 2010), as well as interhemispheric connectivity of the AG with learning to read in late-literate adults (Carreiras et al. 2009). In addition, the posterior part of the SMG, which has some overlap with the angular region of the pIPL, also plays a role in reading (Stoeckel et al. 2009), and activation in the IPL has been found to predict improvement in reading speed after learning French (Barbeau et al. 2017). Thus, stronger interhemispheric pIPL functional connectivity may facilitate communication between the pIPLs and thus support improvement in reading abilities in a language that is being learned.

Interhemispheric connectivity and language

The present investigation indicated that the connectivity between each of the above specific cortical regions with their hemispheric homologues in the other hemisphere may play a role in facilitating specific aspects of the learning of a new language. These findings highlight not only the role of the RH in language learning but also that cooperation between the two hemispheres is beneficial. Although there are competing theories regarding the nature of interhemispheric interactions and whether they are inhibitory or excitatory (see, van der Knaap & van der Ham 2011; Kasselimis & Nidos 2015, for reviews), the evidence appears to indicate that cooperation between the hemispheres is advantageous for performance under demanding conditions (Milner 1980; Banich 1998; Scalf et al. 2009; Höller-Wallscheid et al. 2017). Indeed, Milner (1980) reported a marked deficit in the recall of pictures after unilateral temporal lobectomy, suggesting that the successful recall of much of our past experience normally results from the joint participation of the two cerebral hemispheres. In addition, data from divided visual field experiments show that interhemispheric interaction increases attentional capacity in visual (Banich 1998) and auditory (Scalf et al. 2009) tasks, while fMRI data show that recruitment of homologous regions aids performance in working memory (Höller-Wallscheid et al. 2017). Activation of both hemispheres in various aspects of language processing constitutes evidence that information is being integrated between the two hemispheres, at least in this context (van der Knaap & van der Ham 2011). Such findings could mean that individuals with stronger intrinsic interhemispheric rsFC have the best framework to perform well in challenging conditions, which enables them to acquire efficiently various aspects of a new language.

Interhemispheric connectivity has been implicated in several features of general language processing (see Steinmann & Mulert 2012, for review). Several studies show the importance of interhemispheric interaction for speech comprehension (Beeman et al. 2000; Friederici et al. 2007; Sammler et al. 2010), and differences in individual measures of interhemispheric connectivity have been related to speech perception (Westerhausen et al. 2009). Processing of semantic information compared to perceptual and decision-making information has also been shown to increase interhemispheric cooperation (Perrone-Bertolotti et al. 2013b). In addition, interhemispheric connectivity relates to verbal fluency (Hines et al. 1992). It is of interest to note that there is a relationship between interhemispheric connectivity and the use of more than one language, i.e. bilingualism. One early study examined the interplay between both hemispheres in bilingual individuals and found that, in the initial stages of L2 learning, the RH plays a more significant role but once the L2 has been mastered, the interaction between the two hemispheres is comparable to that in the processing of a native language (L1, Kotik 1983). In terms of structural differences, it has been reported that bilinguals have greater volume in the anterior (Coggins III et al. 2004), mid-anterior and central parts of the CC (Felton et al. 2017), as well as higher FA in the genu, body, and splenium of the CC (Pliatsikas et al. 2015) compared to monolinguals. Other studies have shown that higher functional connectivity between the left and right IFG related to earlier age of L2 acquisition in bilinguals (Berken et al. 2016; Gullifer et al. 2018). Taken together, such findings support the proposal that the cognitive demands of managing multiple languages are reflected in how well the hemispheres are able to communicate. Thus, it also seems reasonable that interhemispheric connectivity supports the ability to acquire and manage knowledge of multiple languages. In fact, although our study focused on predicting learning from pre-existing interhemispheric connectivity, several studies have reported changes in interhemispheric connections in relation to L2 learning skills. Specific connectivity between the left and right IFG appears to contribute to some aspects of language learning aptitude (Xiang et al. 2012), as well as learning of a second language (Qi et al. 2019). In addition, learning of an L2 is associated with higher FA in the genu of the CC (Schlegel et al. 2012) and increases in FC between left and right SMG (Veroude et al. 2010). One study found that faster learners of new phonetic contrasts may have greater interhemispheric connectivity as they tended to have a larger midsagittal area in the middle third of the CC. Furthermore, Antonenko and colleagues (2012) reported that interhemispheric FC between the inferior frontal gyri was negatively correlated with learning of an artificial grammar, although this study was conducted in older adults who may have somewhat different neural connectivity patterns (Goh 2011), and some evidence shows that bilateral recruitment can actually be beneficial for performance in older adults (Wierenga et al. 2008). Overall, the evidence seems to indicate that learning of a new language is one of the conditions under which cooperation between the hemispheres is beneficial for performance. In a recent review, Qi and Legault (2020) point out that "a dynamic bilateral framework involving neural correlates both within and between the two hemispheres underlies the ultimate success of language learning" (p.120).

This idea of a bilateral network involved in language is becoming well established and lends further support to the present findings that interhemispheric connectivity can facilitate L2 acquisition. Indeed, the RH has a significant role in language processing and learning, which is important to understand why interhemispheric cooperation matters in the context of L2 learning. The RH is mainly recognised in language for supra-segmental and abstract language processing (Bottini et al. 1994; Beauregard et al. 1997; Buchanan et al. 2000). More recent studies have shown that the RH can be involved in other aspects of language processing, such as sentence and discourse processing (Gernsbacher & Kaschak 2003; Vigneau et al. 2011). Some have argued that both hemispheres have complementary roles in language processing (Cook 2004). Functional activation in the right frontal and temporal regions has been related to language ability (Van Ettinger-Veenstra et al. 2012). In particular, an early hypothesis explaining the relative role of the hemispheres in the process of L2 acquisition has been that it may mirror that of L1 acquisition in children (Galloway & Krashen 1980; Obler 1981) and that, in the initial stages of learning, there is a shift in laterality from the left to the right hemisphere and a shift back to left hemisphere laterality as proficiency increases. Recent evidence of RH involvement in the early stages of L2 and relationship with L2 proficiency (Reiterer et al. 2009; Qi et al. 2015; Kepinska et al. 2018) appears to support this hypothesis, along with studies that demonstrate aspects of this laterality shift (Hosoda et al. 2013; Xiang et al. 2015; Qi et al. 2019). Thus, the interplay between the hemispheres seems to be a key feature in L2 learning, and it is reasonable that having stronger baseline interhemispheric FC would facilitate this process.

The present study demonstrates that interhemispheric interactions are an important aspect of the L2 learning process and lays the foundation for future investigations into hemispheric dynamics and L2 learning. Future studies using additional measures of language and larger participant samples are necessary to examine further the cooperation of the hemispheres as well as individual patterns of predictors of L2 learning. Moreover, longitudinal studies will be useful to determine whether the relationship between increased interhemispheric FC and L2 improvement persists years after learning and continues to increase with increasing proficiency in the L2 or whether it is a predisposition for better learning abilities that remains stable over time.

Funding:

This work was supported by the Blema and Arnold Steinberg Family Foundation and the Natural Sciences and Engineering Research Council of Canada (D.K.), Canada First Research Excellence Fund, awarded to McGill University for the Healthy Brains for Healthy Lives initiative (X.C.,D.K., S.B. and M.P.), the Canada Research Chairs program (X.C.), the Fonds de Recherche du Québec –Société et Culture (team grant to S.B. and D.K.), the Fonds de Recherche du Québec – Nature et téchnologies and Société et Culture (Centre for Research on Brain, Language and Music), as well as the Jeanne Timmins Costello (JTC) Fellowship (KS).

Notes:

Conflict of Interest: The authors declare no conflict of interest.

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Tables

Table 1. Scores for the English L1 and Mandarin L1 subgroups in working memory and general intelligence, behavioural improvement in French and interhemispheric rsFC. Significance of the group comparisons is reported as a t statistic (p value).

	English L1	Mandarin L1	Significance
Working memory and general intelligence			
Digit Span: Forward (/16)	11.7 ± 1.70	10.25 ± 1.91	1.7 (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)
Improvement in French			
Sentence repetition	11.7 ± 8	7.7 ± 6	1.35 (0.196)
Listening comprehension	17 ± 16.5	11 ± 4.9	1.1 (0.297)
Reading speed	20.3 ± 16.8	14 ± 5.4	1.02 (0.325)
Interhemispheric rsFC			
L - R 45	0.51 ± 0.2	0.65 ± 0.18	-1.48 (0.160)
L - R 44	0.56 ± 0.25	0.65 ± 0.16	-0.8 (0.434)
L - R 9/46v	0.56 ± 0.2	0.4 ± 0.12	1.79 (0.090)
L - R mSTG	1.05 ± 0.29	1.02 ± 0.18	0.26 (0.795)
L - R pIPL	0.78 ± 0.34	0.79 ± 0.19	-0.01 (0.992)

Table 2. MNI coordinates (mm) and volumes (mm³) for the ROIs used.

ROI	Left				Right			
	x	y	z	volume	x	y	z	volume
45	-50	29	19	5197	52	28	18	4306
44	-51	16	25	6170	52	15	26	5504
9/46v	-45	26	33	5784	47	24	32	4456
mSTG	-56	-18	-0.5	16648	56	-19	2	16184
pIPL	-56	-54	28	8208	58	-52	29	7968

Table 3. Mean ± SD for the behavioural measures: percentage of words correctly repeated for sentence repetition, percentage of questions correctly answered for listening comprehension, and words per minute for reading speed. T statistics (p values) [Cohen's d] are also reported.

	Sentence repetition		**Listening comprehension**		**Reading speed**	
	French	English	French	English	French	English
Time 1	26 ± 7.8	97.3 ± 3	11.7 ± 10	10 ± 4.8	74 ± 19.8	169 ± 39
Time 2	36 ± 10	96.8 ± 2	26 ± 16.8	10.8 ± 3.4	91 ± 16	160 ± 32
Significance	-5.68 (<0.00003) [1.12]	0.69 (0.502) [0.20]	-4.77 (<0.0002) [1.03]	-1.05 (0.308) [0.19]	-5.69 (<0.00003) [0.94]	1.76 (0.09) [0.25]

Captions to figures:

Figure 1. Illustration of the ROIs used to extract interhemispheric rsFC in each hemisphere. Area 9/46v and area 44 are in yellow, areas 45 and the mSTG are in red, and the pIPL is in purple. LH = left hemisphere, RH = right hemisphere, mSTG = middle superior temporal gyrus, pIPL = posterior inferior parietal lobule, 9/46v = area 9/46v, 45 = area 45, 44 = area 44.

Figure 2. Relationship between pre-learning (t1) interhemispheric resting-state connectivity of a) area 9/46v and b) area 44 and improvement in sentence repetition (change in percentage of words correctly repeated) with 95% confidence intervals.

Figure 3. Relationship between pre-learning (t1) interhemispheric resting-state connectivity of a) area 45 and b) the mSTG and improvement in listening comprehension (change in percentage of questions correctly answered) with 95% confidence intervals.

Figure 4. Relationship between pre-learning (t1) interhemispheric resting-state connectivity of the pIPL and improvement in reading speed (change in number of words per minute) with 95% confidence intervals.