



Published in final edited form as:

Neuropsychologia. 2018 August ; 117: 123–134. doi:10.1016/j.neuropsychologia.2018.04.037.

Bilingual Experience and Resting-State Brain Connectivity: Impacts of L2 Age of Acquisition and Social Diversity of Language Use on Control Networks

Jason W. Gullifer^{1,2,7,*}, Xiaoqian J. Chai^{3,7}, Veronica Whitford^{4,7}, Irina Pivneva^{1,7}, Shari Baum^{5,7}, Denise Klein^{2,6,7}, and Debra Titone^{1,7,*}

¹Department of Psychology, McGill University

²Cognitive Neuroscience Unit, Montreal Neurological Institute

³Cognitive Neurology/Neuropsychology Division, Department of Neurology, Johns Hopkins University

⁴Department of Psychology, University of Texas at El Paso

⁵School of Communication Sciences and Disorders, McGill University

⁶Department of Neurology and Neurosurgery, McGill University

⁷Centre for Research on Brain, Language and Music, McGill University

Abstract

We investigated the independent contributions of second language (L2) age of acquisition (AoA) and social diversity of language use on intrinsic brain organization using seed-based resting-state functional connectivity among highly proficient French-English bilinguals. There were two key findings. First, earlier L2 AoA related to greater interhemispheric functional connectivity between homologous frontal brain regions, and to decreased reliance on proactive executive control in an AX-Continuous Performance Task completed outside the scanner. Second, greater diversity in social language use in daily life related to greater connectivity between the anterior cingulate cortex and the putamen bilaterally, and to increased reliance on proactive control in the same task. These findings suggest that early vs. late L2 AoA links to a specialized neural framework for processing two languages that may engage a specific type of executive control (e.g., reactive control). In contrast, higher vs. lower degrees of diversity in social language use link to a broadly distributed set of brain networks implicated in proactive control and context monitoring.

*Corresponding author: Department of Psychology, McGill University, 2001 McGill College Ave. Montréal, QC H3A 1G1, jason.gullifer@mail.mcgill.ca.

Publisher's Disclaimer: This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final citable form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

Keywords

bilingualism; resting-state functional connectivity; L2 age of acquisition; social diversity of language use; executive control; brain imaging

1. Introduction

Language use in real-world social contexts requires the dynamic coordination of many interdependent neurocognitive abilities, such as domain-general executive control (Just & Carpenter, 1992; Novick, Trueswell, & Thompson-Schill, 2005; Thompson-Schill, D’Esposito, & Kan, 1999; Thompson-Schill, D’Esposito, Aguirre, & Farah, 1997; Ullman, 2004). People who speak more than one language (i.e., bilinguals), in particular, rely heavily on executive control, as they must relentlessly balance activation of multiple languages across a variety of social contexts (Baum & Titone, 2014; Green & Abutalebi, 2013; Gullifer, Kroll, & Dussias, 2013; Gullifer & Titone, under review; Hopp, 2016; Kroll, Dussias, Bogulski, & Valdés Kroff, 2012; Kroll, Gullifer, & Rossi, 2013; Morales et al., 2016; Pivneva, Mercier, & Titone, 2014; Titone, Gullifer, Subramaniapillai, Rajah, & Baum, 2017; Whitford & Titone, 2012). Accordingly, bilingualism is thought to accompany neural reconfiguration, as brain networks implicated in language become linked to those implicated in executive control (Abutalebi et al., 2013; 2012; Berken, Chai, Chen, Gracco, & Klein, 2016; Coderre, Smith, van Heuven, & Horwitz, 2016; Della Rosa et al., 2012; García-Pentón, Pérez Fernández, Iturria-Medina, Gillon-Dowens, & Carreiras, 2014; Guo, Liu, Misra, & Kroll, 2011; Hernandez, Martinez, & Kohnert, 2000; Klein, Zatorre, Milner, Meyer, & Evans, 1994; Luk, Bialystok, Craik, & Grady, 2011; Mechelli et al., 2004; Pillai et al., 2003; Pliatsikas, Moschopoulou, & Saddy, 2015; Rodriguez-Fornells et al., 2006; see Abutalebi & Green, 2016, for a recent review). Of relevance here, an open question is whether and how the timing of second language (L2) age of acquisition (AoA) and the diversity of social language use independently relate to intrinsic neural connectivity among networks implicated in language and executive control.

1.1. Bilingualism tunes control networks

Because bilinguals must control the simultaneous activation of both languages, even in unilingual social contexts (Dijkstra & van Hell, 2003; Gullifer et al., 2013; Gullifer & Titone, under review; see Whitford, Pivneva, & Titone, 2016, for a recent review), they engage in a variety of domain-general executive control processes, which include response inhibition—mediated by the prefrontal cortex (Green & Eckhardt, 1998; Kroll, Bobb, Misra, & Guo, 2008); attention, monitoring, and error detection—mediated by the anterior cingulate cortex (ACC; Abutalebi et al., 2012; Guo et al., 2011; Rodriguez-Fornells et al., 2006; van Heuven, Schriefers, Dijkstra, & Hagoort, 2008); task switching—mediated by the caudate nucleus (Crinion et al., 2006; Luk, Green, Abutalebi, & Grady, 2012); and maintenance of representations in working memory—mediated by the inferior parietal lobule (IPL; Barbeau et al., 2016; Della Rosa et al., 2012; Mechelli et al., 2004). This distributed network of regions and functions is captured by leading theoretical perspectives, such as the Neurocognitive Language Control Model (NLC model; Abutalebi & Green, 2007; Abutalebi & Green, 2016; Green & Abutalebi, 2013). Importantly, bilinguals are not a

homogeneous group; they vary continuously and dynamically in terms of L2 learning history (such as L2 AoA) and current experience. The NLC model generally deemphasizes the role of L2 AoA in favor of variables related to ongoing experience, though both factors impact brain organization and behavior.

1.1.1. Early L2 AoA strengthens connectivity within frontal brain regions—L2

AoA has fundamental consequences for the structural and resting-state functional organization of the language network, primarily within frontal brain regions (e.g., Berken et al., 2016; Klein, Mok, Chen, & Watkins, 2014; Wartenburger et al., 2003). For example, L2 AoA relates to cortical thickness of and functional connectivity between the left and right inferior frontal gyri (LIFG, RIFG) among highly proficient bilinguals: earlier L2 AoA is associated with a thinner LIFG but thicker RIFG (Klein, et al., 2014), and with increased functional connectivity between the LIFG and RIFG (Berken et al., 2016). Berken et al. (2016) further showed that connectivity between LIFG and RIFG was associated with a reduced reliance on the LIFG during task-based speech production. Thus, early childhood bilingual experience leads to increased connectivity between left and right hemisphere cortical frontal regions involved in, among other things, language and executive control. However, Berken et al. did not explicitly test whether the observed interhemispheric frontal connectivity related to executive control performance in behavior nor did they control for measures of current language experience that are predicted to influence brain organization according to the NLC model.

Other work also suggests a behavioral link between executive control and L2 AoA (see, for example, Kapa & Colombo, 2013; Kousaie, Chai, Sander, & Klein, 2017; Luk, De Sa, & Bialystok, 2011; Pelham & Abrams, 2014; Tao, Marzecová, Taft, Asanowicz, & Wodniecka, 2011). However, in terms of inhibitory control ability, it is unclear whether early bilinguals outperform late bilinguals (Kousaie et al. 2017; Luk et al., 2011), whether late bilinguals outperform early bilinguals (Tao et al., 2011), or whether there are no between-group differences (Pelham & Abrams, 2014). Critically, such studies tend to examine a single mode of inhibitory control—reactive control, that is, the ability to react to and suppress irrelevant information in the moment. Traditional tasks that measure executive control, such as Stroop (Stroop, 1935) and Simon (Simon & Berbaum, 1990), rely on reactive control because each new trial is independent of the prior trial. Yet when there is goal-relevant information encoded in trials that can be used to predict upcoming responses, as in the AX-Continuous Performance Task (AX-CPT; Barch et al., 1997; Braver & Barch, 2002; Carter et al., 1998; Locke & Braver, 2008; Rosvold, Mirsky, Sarason, Bransome, & Beck, 1956), individuals may adopt a proactive strategy and plan responses ahead of time. These two interrelated modes of control are mediated by coordinated activation of the prefrontal cortex and ACC (Braver, Gray, & Burgess, 2007; Braver, Paxton, Locke, Barch, & Smith, 2009; Coderre & van Heuven, 2013; De Pisapia & Braver, 2008; Ullsperger & King, 2010). Importantly, bilingual experience impacts reliance on proactive control measured by the AX-CPT, which coheres with the idea that proactive control may underlie bilinguals' ability to predict upcoming information in different language processing contexts, such as reading (Zirnshtein, van Hell, & Kroll, 2018) and language switching (Zhang, Kang, Wu, Ma, & Guo, 2015). Thus, it is possible that conflicting results regarding L2 AoA and executive control

may be explained, in part, by the examination of a single control mode when, in fact, two modes are at work to greater or lesser degrees. Moreover, given that L2 AoA is a marker of static learning history, it may not fully characterize individuals living in highly bilingual cities, such as Montreal, who have diverse social experiences with respect to language use.

1.1.2. A new marker of current language experience: Social diversity of language use—In Montreal, bilinguals who may be matched on L2 AoA and proficiency can vary greatly in how they use their languages socially (see e.g., Heller, 1982; Higgins, 2004), and they may experience considerable variability in their daily L1 and L2 use across social spheres (Green & Abutalebi, 2013; Hartanto & Yang, 2016). For individuals in these circumstances, differences in L2 AoA may capture some but not all the crucial ways that bilingual experience can relate to brain connectivity and, consequently, behavioral performance. For example, some bilinguals may use their languages in highly integrated social contexts (e.g., communicating in both the L1 and L2 at home and at work), mixing languages frequently within and across contexts. Others may operate in more compartmentalized social contexts (e.g., communicating strictly in the L1 at home and the L2 at work), rarely mixing their languages within a context. The NLC model incorporates the social diversity of language use as a crucial factor that drives neural configuration. It predicts that integrated bilinguals, relative to compartmentalized bilinguals, should adapt stronger connections within the brain networks that mediate a broad set of executive control processes, allowing them to resolve frequent instances of cross-language competition within their social contexts.

While there have been no investigations to date of whether the social diversity of language use is related to resting-state functional connectivity, the NLC model's predictions are borne out in behavior. Factors related to the social diversity of language use, including the tendency to engage in code-switching and language switching, have been shown to modulate behavioral performance on domain-general executive control tasks (Hartanto & Yang, 2016; Hofweber, Marinis, & Treffers-Daller, 2016; Jylkkä et al., 2017; Soveri, Rodriguez-Fornells, & Laine, 2011; Verreyt et al., 2016; see also, Prior & Gollan, 2011). For example, groups of integrated vs. compartmentalized bilinguals show smaller costs associated with non-linguistic task-switching (Hartanto & Yang, 2016), a component of executive control mediated, in part, by subcortical structures (e.g., Crinion et al., 2006; Luk, Green, Abutalebi, & Grady, 2012). Critically, models and empirical studies tend to treat the social diversity of language use dichotomously, when it varies on a continuum, ranging from compartmentalized to integrated. Thus, an open question is how the social diversity of bilingual language use relates to resting-state functional connectivity independently of L2 AoA and how that connectivity, in turn, relates to executive control components that may aid in resolving non-target language activation reactively or proactively in situations where the upcoming language could be predicted on the basis of prior context.

Here, we mathematically formalize the social diversity of language use using information theory (Shannon, 1948). Specifically, the social diversity of language use can be expressed as Shannon entropy, a classic measure of uncertainty, diversity, or disorder. Compartmentalized contexts, where only one language is used the majority of the time, have low diversity (and hence low entropy) with respect to language because the most frequently

used language is highly predictable. In contrast, integrated contexts, where two languages are used in relative balance, have high diversity (and hence high entropy) with respect to language because any given language is highly unpredictable. Thus, language entropy across social spheres can be computed as a continuous measure of social diversity of language use, and can be used as a continuous predictor of both behavior and neural function.

1.2. The present investigation

It is possible that both static historical experiences (i.e., L2 AoA) and ongoing experience in terms of the social diversity of language use (i.e., language entropy) contribute to resting-state functional connectivity. To examine this possibility, we used seed-based resting-state functional connectivity (RSFC), a technique that is highly suited to assessing the impact of real-world language experience on brain organization (Berken et al., 2016; Chai et al., 2016; Fox & Raichle, 2007; Luk, Bialystok, Craik, & Grady, 2011; Whitfield-Gabrieli & Nieto-Castanon, 2012). Specifically, we used RSFC to investigate the relationship between functional connectivity, L2 AoA, and social diversity of language use (i.e., language entropy), focusing on five brain areas implicated in bilingual language control by the NLC model: (1 and 2) BAs 44 and 47 in the LIFG (Luk et al., 2012); (3) ACC (Abutalebi et al., 2012); (4) left caudate (Luk et al., 2012); and (5) left IPL (Barbeau et al., 2016).

On the basis of previous L2 AoA research (e.g., Berken et al., 2016), we predict that after controlling for social diversity of language use, there will be greater interhemispheric connectivity between the LIFG and RIFG related to earlier AoA. On the basis of the NLC model, we further predict that after controlling for L2 AoA, integrated bilinguals with highly diverse social language use (i.e., high entropy; independent of L2 AoA) will have greater connectivity within the networks for language and cognitive control than compartmentalized bilinguals with highly distinct patterns of language use (i.e., low entropy; independent of L2 AoA), reflecting adaptive changes in resting-state connectivity related to the social diversity of language use (Abutalebi & Green, 2016; Green & Abutalebi, 2013). With respect to this last prediction, there are several possible ways that patterns of brain connectivity might link to the social diversity of language use depending on the specific components of executive control that are engaged to a greater or lesser extent for bilinguals with highly diverse social language use.

Across the whole brain, inhibitory control may be achieved through inferior frontal interhemispheric connectivity with the LIFG seed; contextual monitoring may be achieved through connectivity with the ACC seed; task or language switching may be achieved through left caudate connectivity; and cross-language activation may be achieved through connectivity with the left IPL. Indeed, to foreshadow the results, functional connectivity with several of these regions was in fact independently related to L2 AoA and language entropy. As well, the observed functional connectivity was also related to individual differences in reliance on proactive control strategies, as measured by the AX-CPT (e.g., Barch et al., 1997; Carter et al., 1998; Locke & Braver, 2008; Morales et al., 2013; Rosvold et al., 1956) administered outside the scanner.

2. Methods

2.1. Participants

Twenty-eight L1 French - L2 English bilingual adults from McGill University and the surrounding Montreal area were recruited for this study. One participant was excluded due to a missing scan, leaving 27 participants for the analysis (mean age: 23.3 years, *SD*: 3.7, range: 19-32, 10 males, 17 females). Participants completed a language history and demographic questionnaire.

Fourteen participants were born in Quebec (Canada), eleven were born in France, and two were born in the United States (they attended French immersion programs and reported French as their native L1). Participants born outside of Quebec moved to the region for college or university studies (mean age of moving: 19.25 years, *SD*: 2.0, range: 17-23). Participants reported daily use of both languages (mean daily use of L2: 38.9%, *SD*: 14.6, range: 10-70). All participants reported French as their L1 and English as their L2 (mean L2 AoA: 7.5 years, *SD*: 3.7, range: 0-13). Most participants reported knowledge of additional languages besides French or English ($N = 20$). However, only three participants reported daily exposure to those languages and, on average, the degree of exposure was quite low (mean exposure: 5% of the time, *SD*: 3.7, range: 1-10).

All participants were right-handed and had normal or corrected-to-normal visual acuity. Exclusion criteria included language or hearing impairment, any uncorrected visual impairments, history of traumatic brain injury or neurological disorder, and conditions incompatible with magnetic resonance imaging (e.g., metal implants, braces, electronically, magnetically, or mechanically activated devices such as cochlear implants, or claustrophobia).

2.2. Assessing social diversity of language use: Language entropy

To quantify the social diversity of language use in a continuous manner, we computed Shannon entropy associated with proportional L1 and L2 use within each social sphere (i.e., language entropy). This form of entropy provides a measure of diversity, uncertainty, or disorder given a set of probabilistic events, with higher values reflecting greater diversity. As previously mentioned, entropy applies to the social diversity of language use. Compartmentalized contexts carry a low degree of entropy (and thus diversity) with respect to language choice because the appropriate language is highly predictable. In contrast, integrated contexts carry a high degree of entropy because the appropriate language is highly unpredictable.

To compute language entropy, we first extracted data from language history questions on L1 (French) and L2 (English) use in each of three social spheres: home, work¹, and social settings. The six questions elicited Likert responses on a scale from 0 (*none at all*) to six (*all the time*). Within each social sphere, we computed a proportion of L1 and L2 use for each

¹The sample consisted of students from the Montreal area. All but two students reported working. For those two students, mean entropy was calculated on the basis of home and social spheres only. The questionnaire did not include a social sphere related to school.

participant by dividing the Likert score for a given language by the sum of the scores for the two languages. For each social sphere, we computed Shannon entropy (H) using the following equation:

$$H = - \sum_{i=1}^n P_i \log_2(P_i).$$

Here, n represents the total possible languages (i.e., 2) and P_i is the proportion that a given language is used within a social context. We then computed the mean entropy for each participant across social spheres. For a two-language context, language entropy values range from 0 (for a completely predictable compartmentalized context, where only one language is used) to 1 (for an integrated context, where each language is used 50% of the time).

Within spheres, we observed values of language entropy ranging from 0 (no language-related diversity, reflecting compartmentalized language use) to 1 (maximal language-related diversity, reflecting integrated language use). Across spheres (overall), we observed a mean language entropy value of 0.70 (range: 0.41-0.99). Thus, this sample ranged from moderately compartmentalized to fully integrated, which is typical of bilingualism within Montreal. Further, language entropy was not significantly correlated with L2 AoA ($r(25) = -0.32$, $p = 0.10$) in this sample.

2.3. Assessing executive control outside the scanner: AX-CPT

Participants completed a modified version of the AX-CPT outside the scanner (Barch et al., 1997; Carter et al., 1998; Locke & Braver, 2008; Morales et al., 2013; Rosvold et al., 1956). In the AX-CPT, participants view a continuous series of letters, and are instructed to respond “yes” if and only if the current letter is an X and the prior letter was an A , otherwise they respond ‘no’. Crucially, AX conditions occur 70% of the time, establishing a strong impulse to respond “yes” generally over all trials, and particularly when the prior letter is an A or the current letter is an X . As a consequence, two critical “no” conditions provide a way to estimate proactive control, though they do so in opposite ways. In AY conditions, participants first see an A , and then see a non- X letter. To the extent that participants use proactive control to prepare a “yes” response for the subsequent trial upon seeing the A , their performance should suffer when the non- X letter appears and a “no” response is in fact required. In BX conditions, by contrast, participants first see a non- A letter (though in our version, described further below, they always literally see the letter B), and then see an X . To the extent that participants use proactive control to prepare a “no” response for the subsequent trial upon seeing the non- A letter cue, their performance should improve when the X appears. Unlike proactive control, reactive control should always help performance in the moment, and would thereby cancel out for a given individual across AY and BX conditions. Thus, one can obtain a continuous measure from the AX-CPT that reflects how “proactive” a given individual is by subtracting AY performance (in accuracy or correct reaction time) from BX performance, where larger difference scores reflect greater reliance on proactive control.

Given the specific link between bilingualism and shifts toward proactive control (Morales, Gómez-Ariza, & Bajo, 2013; Zhang et al., 2015), we modified our version of the AX-CPT to

enhance the measurement of proactive control (see also Kam, Dominelli, & Carlson, 2012; Li en, Hartmann, Repovš, & Slapni ar, 2016). Normally, *B* cues are randomly selected from various letters of the alphabet on each trial whereas *A* cues consist only of the letter *A*. Because of this, the predictive strength of the *B* cue is more abstract and dilute relative to the *A* cue. To enhance the proactive salience of the *B* cue, we only presented the letter *B*, thereby enabling a more comparable estimation of proactive control between *AY* and *BX* conditions.

2.4. Imaging procedure

Participants were instructed to relax and focus on a fixation cross displayed on a screen in the scanner. Data were acquired on a Siemens 3T TrioTim scanner using a 32-channel head coil. Resting scan images were obtained using a T2-weighted EPI sequence in 42 3.5 mm transverse slices, covering the entire brain (TR: 2210 ms; TE: 30 ms; matrix size: 64 × 64; FOV: 224 mm; flip angle: 90 degrees). A total of 136 slices were obtained in 5 minutes and 9 seconds. Anatomical references were obtained using high-resolution T1-weighted images from a 3D Magnetization Prepared Rapid Gradient Echo (MP-RAGE) sequence (TR: 2300 ms; TE: 2.98 ms; slice thickness: 1 mm; image matrix: 256 × 256; flip angle: 30 degrees; FOV: 256 mm; interleaved excitation).

2.5. Functional connectivity analysis

RSFC data were preprocessed and analyzed using the *CONN toolbox* (version 15h; Whitfield-Gabrieli & Nieto-Castanon, 2012) with SPM12 (Wellcome Department of Imaging Neuroscience, London, UK). Data were preprocessed using the toolbox's default pipeline for volume-based analysis: images were realigned and unwarped, slice-time corrected, segmented and normalized to MNI space, and smoothed with a 6 mm kernel. Head motion was then corrected by identifying problematic time points during the scan using Artifact Detection Tools (ART; http://www.nitrc.org/projects/artifact_detect/). An image was defined as an outlier if the average intensity deviated 3 SDs from the mean intensity in the session or if the composite head movement exceeded 1 mm from the previous image. The composite head movement was computed by first converting six rotation/translation head motion parameters into another set of six parameters characterizing the trajectories of six points located on the center of each of the faces of a bounding box around the brain. The maximum scan-to-scan movement of any of these points was then computed as the single composite movement measure (maximum realignment: 0.79; average realignment: 0.01; neither L2 AoA nor language entropy were associated with realignment; all $t(25) < 1.96$; all $ps > 0.05$). Outlier images were modeled as a covariate (outlier: 1; non-outlier: 0) in the first-level general linear model (GLM) to avoid disrupting the temporal structure of the data. Following artifact detection, spurious noise sources were estimated and regressed out.

Physiological and other spurious sources of noise were estimated and regressed out using the anatomical CompCor method (aCompCor; Behzadi, Restom, Liau, & Liu, 2007). Global signal regression (Murphy, Birn, Handwerker, Jones, & Bandettini, 2009; Saad et al., 2012) was not used. Five principal components of signals from white matter and cerebrospinal fluid regions of interest (ROIs) were regressed out. Residual head motion parameters (three

rotation, three translation, and six first-order derivatives) were also regressed out. A temporal bandpass filter (0.008 - 0.09 Hz) was applied to the time series. Next, the data were entered into first- and second-level analyses.

The functional connectivity analysis was performed using a seed-driven, ROI approach. Seed-voxel correlations were computed by estimating temporal correlations between the blood oxygen level-dependent (BOLD) signal from our a priori ROIs (seeds) and the BOLD signal at every other brain voxel. We chose five seeds that have been implicated in bilingual language processing and control by the NLC model (Abutalebi & Green, 2007): two seeds in the LIFG (left BA 44 and BA 47; Luk et al., 2012), one in the ACC (BA 24; Abutalebi et al., 2012), one in the left caudate (Luk et al., 2012), and one in the left IPL (BA 40; Barbeau et al., 2016). See Table 1 for seed coordinates. First-level correlation maps were produced by extracting the residual BOLD time course from each seed and computing Pearson's correlation coefficients between that time course and the time course of all other voxels. Coefficients were converted to z-scores using Fisher's transformation to allow for second-level GLM analyses. For second-level analyses, first-level connectivity maps for each participant were entered into whole-brain regression analyses to determine brain regions that showed a significant relationship between resting-state connectivity strength and the variables of interest: L2 AoA and language entropy. For each seed, we computed a statistical model that included L2 AoA and language entropy, allowing us to assess the independent contribution of each variable of interest.

All reported clusters survived the threshold of $p < 0.05$ using a false-discovery rate correction with a peak voxel-level significance threshold of $p < 0.001$ (uncorrected). Cluster coordinates are reported in MNI space together with the cluster size.

3. Results

3.1. Behavioral analysis of the AX-CPT

Participants were highly accurate on the AX-CPT ($M_{\text{Overall}} = 95\%$; $M_{\text{AX}} = 97\%$; $M_{\text{AY}} = 86\%$; $M_{\text{BX}} = 88\%$; $M_{\text{BY}} = 100\%$). As such, we focused our statistical analysis on correct reaction times². We analyzed trial-level data in R (R Core Team, 2017) using linear mixed-effects regression models in the *lme4* package (Bates, Mächler, Bolker, & Walker, 2015), with random intercepts for participant and random slopes for condition by participant. The baseline condition was set as the *AY* condition, allowing us to contrast performance on *BX* trials relative to *AY* trials to provide a measure of proactive control shift. Significance for inclusion of effect terms and interactions was evaluated through an Analysis of Variance via the *anova()* function in the *lmerTest* package using the Satterthwaite approximation (Kuznetsova, Brockhoff, & Christensen, 2016).

Condition (four levels: *BY*, *AY*, *BX*, *AX*) significantly predicted reaction times on the AX-CPT ($F(3, 32.76) = 73.06$, $p < 0.001$). Response times to the *BX* condition were significantly faster than the *AY* condition ($\beta = -0.27$, $SE = 0.07$, $t = -4.18$, $p < 0.001$), indicating an overall proactive control strategy.

²Statistical models for accuracy showed the same general pattern of results.

In a follow-up model, we added interactions between L2 AoA and condition, and between language entropy and condition, to test whether these experiential factors modulated executive control strategies. Given that we included individual difference measures in this analysis, we removed the random slopes for condition to ensure that individual differences could be captured in the fixed effects analysis. Both L2 AoA and language entropy significantly interacted with condition (L2 AoA * Condition: $F(3, 3058.37) = 7.71, p < 0.001$; language entropy * Condition: $F(3, 3058.30) = 6.54, p < 0.001$). Participants with early L2 AoA had a smaller speed advantage for *BX* trials relative to *AY* trials ($\beta = -0.13, SE = 0.03, t = -4.61, p < 0.001$), indicating that they had decreased reliance on proactive control relative to participants with late L2 AoA. Participants with higher language entropy had a greater speed advantage for *BX* trials relative to *AY* trials ($\beta = -0.11, SE = 0.03, t = -4.21, p < 0.001$), indicating that they had increased reliance on proactive control.

3.2. RSFC analysis: Influence of L2 AoA controlling for social diversity of language use (language entropy)

Functional connectivity was associated with L2 AoA after controlling for language entropy. Of interest, connectivity between the LIFG (BA 44) and homologous clusters of the RIFG was inversely related to L2 AoA (see Figure 1). Connectivity between these areas was stronger for participants with earlier L2 AoA relative to those with later L2 AoA. This pattern of results held after controlling for self-reported daily L2 use. The pattern of results also held when we used non-parametric permutation tests (1000 samples), which may help guard against false-positives in neuroimaging analyses with respect to parametric tests (e.g., Eklund, Nichols, Knutsson, 2016). See Table 2 for the full set of results related to L2 AoA.

3.3. RSFC analysis: Influence of social diversity of language use (language entropy) controlling for L2 AoA

Functional connectivity was associated with social diversity of language use (language entropy) after controlling L2 AoA. Participants with more language entropy had greater functional connectivity between the ACC (BA 24) and clusters in the putamen bilaterally (see Figure 2). Furthermore, these participants had greater connectivity between the left caudate and clusters bilaterally in the superior temporal gyrus (STG), including the planum temporale and BA 41/42 (see Figure 3). This pattern of results held after controlling for self-reported daily L2 use. The pattern of results also held when we used non-parametric permutation tests (1000 samples). See Table 3 for the full set of results related to social diversity of language use.

3.4. Relationship between functional connectivity and AX-CPT performance

Given that the bilateral prefrontal cortex and ACC are implicated in bilingual language control (Abutalebi & Green, 2007; Abutalebi & Green, 2016; Green & Abutalebi, 2013) and in shifts between reactive and proactive control (Braver, et al., 2009; Ullsperger & King, 2010), we extracted the connectivity values between the LIFG and RIFG, and between the ACC and each of the putamen clusters for each participant. We then entered these values into the multiple regression analysis of the AX-CPT data (see Table 4 for the fixed-effects from the mixed effects model).

LIFG-RIFG connectivity and ACC-left putamen connectivity interacted with condition, while ACC-right putamen connectivity did not (LIFG-RIFG * condition: $F(3, 3055.24) = 13.01, p < 0.001$; ACC-left putamen * condition: $F(3, 3055.18) = 4.06, p < 0.01$; ACC-right putamen * condition: $F(3, 3055.32) = 1.31, p > 0.05$). Specifically, greater LIFG-RIFG connectivity (which was associated with early L2 AoA) was associated with a smaller speed advantage for *BX* vs. *AY* trials ($\beta = 0.16, SE = 0.03, t = 6.00, p < 0.001$), reflecting reduced reliance on proactive control. See Figure 1C for an illustration of the results. Greater ACC-left putamen connectivity (which was associated with more language entropy) was associated with a greater speed advantage for *BX* vs. *AY* trials ($\beta = -0.10, SE = 0.04, t = -2.27, p < 0.05$), reflecting increased reliance on proactive control. See Figure 2C for an illustration of the results.

4. Discussion

An open question within the cognitive neuroscience of bilingualism is how different aspects of real-world bilingual history and experience link to resting-state connectivity of the brain networks implicated in language and executive control. Static historical measures of experience such as L2 AoA are well-studied, but other measures such as the social diversity of language use are just gaining attention in the literature. Here, we examined the independent contributions of L2 AoA and diversity of language use (i.e., language entropy) across social spheres in modulating the functional connectivity between regions involved in language and executive control based on influential neurocognitive models (Abutalebi & Green, 2007, 2016; Green & Abutalebi, 2013). We found that both variables related to independent patterns of functional connectivity: L2 AoA modulated connectivity between classic frontal regions, whereas language entropy modulated connectivity between a more diverse set of regions, spanning frontal, subcortical, and temporal areas. These results suggest that both static acquisition history and the social diversity of language use contribute to adaptive changes in brain networks involved in bilingual language control³.

We found that early L2 AoA was associated with stronger connectivity between left and right prefrontal regions, when social diversity of language use was statistically controlled. In particular, L2 AoA modulated functional connectivity between the LIFG and RIFG: connectivity was greater for early vs. late L2 AoA bilinguals. The NLC model (Abutalebi & Green, 2007, 2016; Green & Abutalebi, 2013) implicates the LIFG and RIFG as key areas in the bilingual language control system; however, the model does not make specific predictions about whether L2 AoA should modulate these connections. Yet, the finding here is consistent with previous work by Berken et al. (2016) showing that simultaneous and early bilinguals have increased bilateral frontal connectivity between highly similar regions. Moreover, this work extends that of Berken et al. in two major ways. First, it replicates the relationship between static learning history and frontal brain connectivity, even after controlling for a previously untested factor that is predicted by the NLC model to critically impact bilingual brain organization: the social diversity of language use. Second, it provides

³It is also possible that the two measures of language experience jointly contribute to resting-state connectivity. We tested this hypothesis in a post-hoc analysis by including an interaction term between L2 AoA and language entropy for each of the seed-based models. After the interaction term was included, the general pattern of results for the main effects of L2 AoA and language entropy did not change. Moreover, there was limited evidence for interactions between L2 AoA and language entropy.

a link between the observed frontal connectivity and behavioral measures of executive control mediated, in part, by prefrontal areas including the LIFG and RIFG.

The LIFG is a classic language area located in the prefrontal cortex, and the pars opercularis constitutes part of Broca's area. Both the LIFG and the RIFG are involved in domain-general cognitive control, including reactive and proactive control (e.g., Braver, 2012; Braver et al., 2007; 2009; Coderre & van Heuven, 2013; De Pisapia & Braver, 2008; Ullsperger & King, 2010). Moreover, the RIFG (including the pars opercularis) is implicated in response inhibition, is likened to a cognitive brake that slows or suppresses a pre-potent response, and has been implicated during the voluntary blocking of memory retrieval (for reviews on the RIFG, see Aron, Robbins, & Poldrack, 2004, 2014).

Response inhibition is a mechanism central to bilingual language selection in production (Green & Eckhardt, 1998; Guo et al., 2011; Kroll et al., 2008; Levy, McVeigh, Marful, & Anderson, 2007; Meuter & Allport, 1999) and comprehension (Macizo, Bajo, & Martín 2010; Pivneva et al., 2014), as selection of words in the target language involves inhibition of co-activated words in the unintended language. Although inhibitory control is thought to be recruited over the short-term to regulate cross-language activation (either reactively or proactively), long-term impacts of inhibitory control are also evident in behavior. For example, college-aged L2 learners immersed in the L2 over several months have been shown to have reduced lexical access in their L1 relative to un-immersed learners (Linck, Kroll, & Sunderman, 2009), suggesting that the L1 becomes inhibited more globally in the long-term. At present, there is debate regarding the extent to which inhibitory control mechanisms continue to be recruited among highly proficient bilinguals (e.g., Costa, Santesteban, & Ivanova, 2006), whether continuous recruitment of inhibitory control for language improves domain-general mechanisms (e.g., Paap & Greenberg, 2013), and whether these neurofunctional processes further depend on other factors such as L2 AoA and the social diversity of language use (e.g., Green & Abutalebi, 2013; Kapa & Colombo, 2013; Kousaie, et al., 2017; Luk, De Sa, & Bialystok, 2011; Pelham & Abrams, 2014; Tao, Marzecová, Taft, Asanowicz, & Wodniecka, 2011). Here, differential connectivity between frontal regions for early vs. late L2 AoA bilinguals provides additional evidence that the precise timing of exposure to an L2 early on in life indeed impacts how the inhibitory control network is adapted to regulate the two language systems among highly proficient bilinguals in a manner that is independent of current experience (such as the social diversity of language use).

Consistent with this hypothesis, we observed a relationship between LIFG-RIFG connectivity and AX-CPT behavioral performance. Greater LIFG-RIFG connectivity (present in early L2 AoA bilinguals) was related to less reliance on proactive control, reflected in a reduced AY-BX difference score. Participants with greater LIFG-RIFG connectivity showed less evidence of using the highly predictive *B* cue proactively to plan a subsequent “no” response to the *X* letter. These participants had decreased performance (slower reaction times) in responding “no” to highly frequent *X* letters (that typically require a “yes” response) in *BX* conditions, despite the presence of the *B* letter that cues the “no” response. Instead, these participants likely relied on reactive control in the moment to complete the task, perhaps by engaging the RIFG as a cognitive brake to inhibit the pre-potent “yes” response when presented with the highly-frequent *X* letter. In contrast, less

connectivity between these frontal regions (present in late L2 AoA bilinguals) was associated with a shift towards proactive control, that is, the use of contextual information to preemptively plan a forthcoming response. On *BX* conditions, participants with less connectivity used the presence of a highly predictive *B* cue to make a speedy “no” response to the *X* letter, resulting in a large *AY-BX* difference score. In other words, late L2 AoA bilinguals were more likely to proactively inhibit the pre-potent response and may also be less reliant on reactive control and the RIFG relative to early L2 AoA bilinguals.

Thus, one interpretation of these results is that the early acquisition of two languages in childhood promotes a bilingual neural framework in which greater functional separation of those languages in real time is achieved through reactive inhibitory control, mediated by interhemispheric connectivity in the inferior frontal cortices. In contrast, the later acquisition of an L2 requires folding a new language system into an already existing left-hemisphere dominant network that is tuned for one language (Hernandez, Li, & MacWhinney, 2005; Klein et al., 2014). This may, in turn, require a more diverse set of executive control processes (e.g., proactive control) to functionally separate the two languages in real time. This interpretation coheres with recent data showing similar patterns of cortical thickness for simultaneous bilinguals relative to monolinguals, but greater cortical thickness in the LIFG when the L2 is acquired later (Klein et al., 2014). These results relate to previous studies showing that early L2 AoA may lead to greater *bilingual advantages* in resolving interference as measured by reactive control tasks, such as the Simon and Flanker tasks (e.g., Kousaie et al., 2017; Luk, De Sa, & Bialystok, 2011).

Indeed, the term *bilingual advantage* stems from early findings that bilinguals experience less costly interference effects relative to monolinguals on reactive inhibitory control tasks, such as the Simon task (e.g., Bialystok, Craik, Klein, & Viswanathan, 2004), suggesting that they have superior executive control abilities. However, bilingual advantage effects are not always straightforward, and some researchers fail to find effects of bilingual experience on general cognitive function (e.g., Paap & Greenberg, 2013). Crucially, the way in which neurocognitive tuning manifests may depend on the specific cognitive components measured by the task and extent to which the type of bilingual experience leads to the recruitment of those components (Baum & Titone, 2014; Titone et al., 2017). In other words, not all difference scores are equal, and not all bilinguals are equal. When a proactive component is introduced to a task (such as in AX-CPT), the nature of the difference score changes, and it becomes difficult to identify “superior” performance. Although we indeed observed a reduction in the difference score between *AY* and *BX* conditions that related to LIFG-RIFG connectivity and to early L2 AoA, this reduction was, in fact, driven by a slowdown for *BX* conditions, as these participants shifted away from a proactive strategy. Thus, early L2 AoA may be beneficial for inhibitory control in reactive tasks; however, it may impede performance when that task requires proactive control. Moreover, day-to-day experience in using the two languages may further drive the recruitment of different neurocognitive components (Abutalebi & Green, 2016), which was another primary focus of this study.

In contrast to the static experience variable (i.e., L2 AoA), the social diversity of language use, operationally defined as language entropy, modulated resting-state connectivity for a widespread set of regions. Connectivity between the ACC and bilateral putamen, and

between the left caudate and bilateral STG, was stronger for integrated bilinguals with greater language entropy. Generally, the NLC model implicates all of these areas, save the STG, as key areas in bilingual language and executive control. These novel findings corroborate recent behavioral investigations showing that the social diversity of language use impacts performance on domain general executive control tasks, including language and task switching (Hartanto & Yang, 2016; Hofweber, Marinis, & Treffers-Daller, 2016; Jylkkä et al., 2017; Soveri, Rodriguez-Fornells, & Laine, 2011; Verreyt et al., 2016; see also, Prior & Gollan, 2011).

The ACC has been implicated in monitoring, conflict resolution, and language switching. The putamen has been implicated in speech articulation of the nondominant language (Abutalebi et al., 2013; Klein et al., 1994; Price, 2010). The links between these two regions may reflect greater necessity among more integrated bilinguals to monitor environments, for which language use is uncertain and in which there is frequent competition between the two languages, to allow them to switch articulatory repertoire when necessary. Recall that integrated bilingual social use is associated with high language diversity (i.e., entropy). One way that bilinguals in such contexts might adapt to uncertainty is through attention to linguistic cues present in the environment. To illustrate, knowledge that a particular coworker prefers one language over the other might help reduce language-related uncertainty when interacting with that coworker in an otherwise bilingual environment. Language cues have been studied extensively in the literature on code-switching. Code-switching is a consequence of integrative bilingualism in which bilinguals switch languages with one another within or across an utterance (e.g., Lipski, 1978, 1985; Poplack, 1980). Crucially, code-switching is not a random behavior; it is a process that is governed by several factors (or cues) including sociolinguistic considerations (Kootstra, van Hell, & Dijkstra, 2010), grammatical patterns (Di Sciullo, Muysken, & Singh, 1986; Kootstra et al., 2010; Lipski, 1985; Myers-Scotton, 1993; Poplack, 1980), lexical processes (Broersma, 2009; Kootstra, van Hell, & Dijkstra, 2012), and patterns of language use in the environment (Valdés Kroff, Dussias, Gerfen, Perrotti, & Bajo, 2016). Thus, integrative bilingualism overall, and in particular integrative bilingualism that involves predictable instances language switching like code-switching, may strengthen monitoring and switching components of executive control, including proactive strategies that emphasize attention to and maintenance of contextual information.

Consistent with these hypotheses, we observed a relationship between ACC-left putamen connectivity and behavioral performance on the AX-CPT. Greater connectivity (present in integrated bilinguals with more language entropy) was associated with a shift towards the use of proactive control strategies, marked by an increase in the *AY-BX* difference score. Participants with greater ACC-putamen connectivity showed more evidence of using the highly predictive *B* cue proactively to plan and execute a speedy “no” response to the *X* letter. In contrast, less connectivity (present in compartmentalized bilinguals with less language entropy) was associated with a shift away from proactive control, marked by an increase in *BX* decision times, suggesting that participants with less connectivity relied on reactive control processes. Thus, repeated experiences within particular social contexts of bilingualism appear to adaptively tune executive control processes and brain networks that are likely to be recruited within those contexts.

The social diversity of language use also predicted functional connectivity between the left caudate and the STG bilaterally, particularly clusters in the planum temporale (BA41/42). The caudate is a region implicated in language control and language switching. The clusters in the bilateral STG, while not specifically implicated in bilingual language control, include part of Wernicke's area in the left hemisphere and its homologue in the right hemisphere. Both areas are considered core regions for language processing more generally. Wernicke's area is involved in the processing of meaning and sensory information (DeWitt & Rauschecker, 2013; Shapleske, Rossell, Woodruff, & David, 1999), and is connected to frontal areas implicated in motor output via the arcuate fasciculus (Catani & Mesulam, 2008; Geschwind, 1970). Thus, integrative bilingualism may relate to stronger connectivity between areas involved in language switching and those that link sensory information to motor output.

The link between brain areas involved in switching and areas that link sensory information to motor output is particularly relevant in the context of recent behavioral work on nonlinguistic task switching in bilinguals (Hartanto & Yang, 2016; Prior & MacWhinney, 2010). Diffusion model analyses by Hartanto and Yang (2016) show a bilingual advantage (relative to monolinguals) in task switching that is more pronounced for integrated vs. compartmentalized bilinguals. Crucially, the advantage arises in non-decision time, a component of response time that reflects the ability to shift between sensory analysis and motor output (Rogers & Monsell, 1995). These results, together with those of the present study, suggest that integrated social contexts influence behavioral and neural efficiency associated with task-set reconfiguration—the ability to shift task-sets in response to a new task (or language).

The right homologue of Wernicke's area is also involved in semantic processing, particularly in the processing and resolution of subordinate meanings of ambiguous words (Harpaz, Levkovitz, & Lavidor, 2009; Peretz & Lavidor, 2013). Greater connectivity between an area implicated in language switching/control and one involved in the resolution of ambiguity for integrated bilinguals is noteworthy, as one of the hallmarks of bilingual language processing is the simultaneous co-activation of lexical alternatives in both languages, even when only one language is required (e.g., Dijkstra & van Hell, 2003; Gullifer et al., 2013; Gullifer & Titone, under review; see Whitford et al., 2016, for a recent review). Hence, for a bilingual, any given word is, in a way, ambiguous because it has a corresponding translation equivalent that becomes momentarily co-activated in the other language. While no studies to date have explicitly examined the role of the social diversity of language use on cross-language activation, language switches in the moment do appear to increase phonological and lexical competition between languages (Filippi, Karaminis, & Thomas, 2013; Goldrick, Runnqvist, & Costa, 2014; Olson, 2013). Thus, integrative contexts may increase the degree of cross-language co-activation, requiring more extensive recruitment of control processes to cope with this co-activation. Under a traditional view of bilingual language control, resolution of this co-activation might proceed through the engagement of inhibitory control in the moment. However, under accounts that posit two modes of control (Braver, Gray, & Burgess, 2007; Braver, Paxton, Locke, Barch, & Smith, 2009), it is possible that proactive control becomes engaged to preemptively select the intended meaning from a pool of co-activated alternatives.

In sum, we used resting-state functional connectivity combined with behavior as a tool to explore the effects of static and changing language experience on the wiring of the brain. Such an approach is optimal for observing networks of connectivity in relation to performance, but is limited in relating the role of specific functions to specific brain regions. In our study, however, the observed relationships between connectivity patterns and behavior, in conjunction with the results of previous behavioral and neuroimaging studies, do provide converging evidence for the claims discussed above. Future studies associating task-based functional imaging and resting-state connectivity data should elucidate these relationships more clearly.

Overall, the present findings corroborate recent theoretical perspectives on bilingual language control, including the NLC model (Abutalebi & Green, 2007) and the Adaptive Control Hypothesis (ACH; Green & Abutalebi, 2013). The NLC model emphasizes the role of bilingual experience in organizing brain networks related to language and executive control throughout the lifespan (i.e., from early childhood through late adulthood), while the ACH further proposes that the organization of this network can be adapted to suit the needs of the social diversity of language use (e.g., compartmentalized situations that dictate the use of one language vs. integrative situations that require the use of multiple languages). Consistent with these perspectives, we found that the functional connectivity between core areas of the neurocognitive language control model (i.e., ACC, basal ganglia, and IFG) was related to bilingual experience. Notably, connectivity within this network was modulated by static factors that mark language acquisition during formative years and a factor related to ongoing real-world social language use during adulthood. Future work should investigate potential interactions between static experience and ongoing experience, as static experience may, in some regards, drive ongoing experience. For example, here there was a non-significant trend suggesting that early L2 AoA may lead to higher social diversity of language usage. Models such as the NLC and ACH are fruitful in that they provide the scaffolding to account for the full range of bilingual experience, as seen in highly bilingual cities such as Montreal, Canada.

Acknowledgments

This work was supported by the Natural Sciences and Engineering Research Council of Canada (individual Discovery Grants, 03911 to Baum, 05371 to Klein, & 264146 to Titone); the National Institutes of Health (Postdoctoral training grant, F32-HD082983 to Gullifer, Titone, and Klein); the Centre for Research on Brain, Language & Music; and the Blema and Arnold Steinberg Family Foundation.

References

- Abutalebi J, Green D. Bilingual language production: The neurocognition of language representation and control. *Journal of Neurolinguistics*. 2007; 20(3):242–275. DOI: 10.1016/j.jneuroling.2006.10.003
- Abutalebi J, Green DW. Neuroimaging of language control in bilinguals: neural adaptation and reserve. *Bilingualism: Language and Cognition*. 2016; 19(4):689–698. DOI: 10.1017/S1366728916000225
- Abutalebi J, Rosa Della PA, Castro Gonzaga AK, Keim R, Costa A, Perani D. The role of the left putamen in multilingual language production. *Brain and Language*. 2013; 125(3):307–315. DOI: 10.1016/j.bandl.2012.03.009 [PubMed: 22538086]

- Abutalebi J, Rosa Della PA, Green DW, Hernandez M, Scifo P, Keim R, et al. Bilingualism tunes the anterior cingulate cortex for conflict monitoring. *Cerebral Cortex*. 2012; 22:2076–2086. DOI: 10.1093/cercor/bhr287 [PubMed: 22038906]
- Aron AR, Robbins TW, Poldrack RA. Inhibition and the right inferior frontal cortex. *Trends in Cognitive Sciences*. 2004; 8(4):170–177. DOI: 10.1016/j.tics.2004.02.010 [PubMed: 15050513]
- Aron AR, Robbins TW, Poldrack RA. Inhibition and the right inferior frontal cortex: one decade on. *Trends in Cognitive Sciences*. 2014; 18(4):177–185. DOI: 10.1016/j.tics.2013.12.003 [PubMed: 24440116]
- Barbeau EB, Chai XJ, Chen JK, Soles J, Berken J, Baum S. , et al. The role of the left inferior parietal lobule in second language learning: An intensive language training fMRI study. *Neuropsychologia*. 2016.
- Barch DM, Braver TS, Nystrom LE, Forman SD, Noll DC, Cohen JD. Dissociating working memory from task difficulty in human prefrontal cortex. *Neuropsychologia*. 1997; 35(10):1373–1380. DOI: 10.1016/S0028-3932(97)00072-9 [PubMed: 9347483]
- Bates D, Mächler M, Bolker B, Walker S. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*. 2015; 67(1)doi: 10.18637/jss.v067.i01
- Baum S, Titone D. Moving toward a neuroplasticity view of bilingualism, executive control, and aging. *Applied Psycholinguistics*. 2014; 35(05):857–894.
- Behzadi Y, Restom K, Liao J, Liu TT. A component based noise correction method (CompCor) for BOLD and perfusion based fMRI. *NeuroImage*. 2007; 37(1):90–101. DOI: 10.1016/j.neuroimage.2007.04.042 [PubMed: 17560126]
- Berken JA, Chai X, Chen JK, Gracco VL, Klein D. Effects of Early and Late Bilingualism on Resting-State Functional Connectivity. *The Journal of Neuroscience*. 2016; 36(4):1165–1172. DOI: 10.1523/JNEUROSCI.1960-15.2016 [PubMed: 26818505]
- Bialystok E, Craik FIM, Klein R, Viswanathan M. Bilingualism, aging, and cognitive control: evidence from the Simon task. *Psychology and Aging*. 2004; 19(2):290–303. [PubMed: 15222822]
- Braver TS. The variable nature of cognitive control: a dual mechanisms framework. *Trends in Cognitive Sciences*. 2012; 16:106–113. [PubMed: 22245618]
- Braver TS, Barch DM. A theory of cognitive control, aging cognition, and neuromodulation. *Neuroscience and Biobehavioral Reviews*. 2002; 26:809–817. [PubMed: 12470692]
- Braver TS, Gray JR, Burgess GC. Explaining the Many Varieties of Working Memory Variation: Dual Mechanisms of Cognitive Control. In: Conway A, Jarrold C, Kane M, Miyake A, Towse J, editors *Variation in Working Memory*. New York, NY: Oxford University Press; 2007. 76–106.
- Braver TS, Paxton JL, Locke HS, Barch DM, Smith EE. Flexible Neural Mechanisms of Cognitive Control within Human Prefrontal Cortex. *Proceedings of the National Academy of Sciences of the United States of America*. 2009; 106(18):7351–7356. DOI: 10.2307/40483276?ref=search-gateway:3d23b95a96418abe2538fec10811203e [PubMed: 19380750]
- Broersma M. Triggered codeswitching between cognate languages. *Bilingualism: Language and Cognition*. 2009; 12(04):447–462. DOI: 10.1017/S1366728909990204
- Carter CS, Braver TS, Barch DM, Botvinick MM, Noll D, Cohen JD. Anterior cingulate cortex, error detection, and the online monitoring of performance. *Science*. 1998; 280(5364):747–749. [PubMed: 9563953]
- Catani M, Mesulam M. The arcuate fasciculus and the disconnection theme in language and aphasia: History and current state. *Cortex*. 2008; 44(8):953–961. DOI: 10.1016/j.cortex.2008.04.002 [PubMed: 18614162]
- Chai XJ, Berken JA, Barbeau EB, Soles J, Callahan M, Chen JK, Klein D. Intrinsic Functional Connectivity in the Adult Brain and Success in Second-Language Learning. *The Journal of Neuroscience*. 2016; 36(3):755–761. DOI: 10.1523/JNEUROSCI.2234-15.2016 [PubMed: 26791206]
- Coderre EL, Smith JF, van Heuven WJB, Horwitz B. The functional overlap of executive control and language processing in bilinguals. *Bilingualism: Language and Cognition*. 2016; 19:471–488.
- Coderre EL, van Heuven WJB. Modulations of the executive control network by stimulus onset asynchrony in a Stroop task. *BMC Neuroscience*. 2013; 14:1–18. [PubMed: 23280045]

- Costa A, Santesteban M, Ivanova I. How do highly proficient bilinguals control their lexicalization process? Inhibitory and language-specific selection mechanisms are both functional. *Journal of Experimental Psychology: Learning, Memory, and Cognition*. 2006; 32(5):1057–1074. DOI: 10.1037/0278-7393.32.5.1057
- Crinion J, Turner R, Grogan A, Hanakawa T, Noppeney U, Devlin JT, et al. Language control in the bilingual brain. *Science*. 2006; 312(5779):1537–1540. DOI: 10.2307/3846323?ref=search-gateway:847b348178230404c3274f1743994766 [PubMed: 16763154]
- Della Rosa PA, Videsott G, Borsa VM, Canini M, Weekes BS, Franceschini R, Abutalebi J. A neural interactive location for multilingual talent. *Cortex*. 2012; 49(2):605–608. DOI: 10.1016/j.cortex.2012.12.001 [PubMed: 23294573]
- De Pisapia N, Braver TS. A model of dual control mechanisms through anterior cingulate and prefrontal cortex interactions. *Neurocomputing*. 2006; 69:1322–1326.
- DeWitt I, Rauschecker JP. Wernicke's area revisited: Parallel streams and word processing. *Brain and Language*. 2013; 127(2):181–191. DOI: 10.1016/j.bandl.2013.09.014 [PubMed: 24404576]
- Dijkstra T, van Hell JG. Testing the language mode hypothesis using trilinguals. *International Journal of Bilingual Education and Bilingualism*. 2003; 6(1):37–41 h. DOI: 10.1080/13670050308667769
- Di Sciullo AM, Muysken P, Singh R. Government and code-mixing. *Journal of Linguistics*. 1986; 22(1):1–24. DOI: 10.1017/S0022226700010537
- Eklund A, Nichols TE, Knutsson H. Cluster failure: why fMRI inferences for spatial extent have inflated false-positive rates. *Proceedings of the National Academy of Sciences*. 2016; 113(28):7900–7905.
- Filippi R, Karaminis T, Thomas MSC. Language switching in bilingual production: Empirical data and computational modelling. *Bilingualism: Language and Cognition*. 2013; 17(2014):294–315. DOI: 10.1017/S1366728913000485
- Fox MD, Raichle ME. Spontaneous fluctuations in brain activity observed with functional magnetic resonance imaging. *Nature Reviews Neuroscience*. 2007; 8(9):700–711. DOI: 10.1038/nrn2201 [PubMed: 17704812]
- García-Pentón L, Pérez Fernández A, Iturria-Medina Y, Gillon-Dowens M, Carreiras M. Anatomical connectivity changes in the bilingual brain. *NeuroImage*. 2014; 84:495–504. DOI: 10.1016/j.neuroimage.2013.08.064 [PubMed: 24018306]
- Geschwind N. The organization of language and the brain. 1970
- Goldrick M, Runnqvist E, Costa A. Language switching makes pronunciation less nativelike. *Psychological Science*. 2014; 25(4):1031–1036. DOI: 10.1177/0956797613520014 [PubMed: 24503870]
- Green DW, Abutalebi J. Language control in bilinguals: The adaptive control hypothesis. *Journal of Cognitive Psychology*. 2013; 25(5):515–530. DOI: 10.1080/20445911.2013.796377 [PubMed: 25077013]
- Green DW, Eckhardt V. Mental control of the bilingual lexico-semantic system. *Bilingualism: Language and Cognition*. 1998; 1(2):67–81. DOI: 10.1017/S1366728998000133
- Gullifer JW, Kroll JF, Dussias PE. When language switching has no apparent cost: Lexical access in sentence context. *Frontiers in Psychology*. 2013; 4:1–13. DOI: 10.3389/fpsyg.2013.00278 [PubMed: 23382719]
- Gullifer JW, Titone D. The impact of a momentary language switch on bilingual reading: Intense at the switch but merciful downstream for L2 but not L1 readers. (under review).
- Guo T, Liu H, Misra M, Kroll JF. Local and global inhibition in bilingual word production: fMRI evidence from Chinese-English bilinguals. *NeuroImage*. 2011; 56(4):2300–2309. DOI: 10.1016/j.neuroimage.2011.03.049 [PubMed: 21440072]
- Harpaz Y, Levkovitz Y, Lavidor M. Lexical ambiguity resolution in Wernicke's area and its right homologue. *Cortex*. 2009; 45(9):1097–1103. DOI: 10.1016/j.cortex.2009.01.002 [PubMed: 19251255]
- Hartanto A, Yang H. Disparate bilingual experiences modulate task-switching advantages: A diffusion-model analysis of the effects of interactional context on switch costs. *Cognition*. 2016; 150:10–19. DOI: 10.1016/j.cognition.2016.01.016 [PubMed: 26848731]

- Heller MS. “Bonjour, Hello?.”: Negotiations of language choice in Montreal. In: Gumperz J, Cook-Gumperz J, editors *Language and Social Identity*. Cambridge: Cambridge University Press; 1982. 108–118.
- Hernandez A, Li P, MacWhinney B. The emergence of competing modules in bilingualism. *Trends in Cognitive Sciences*. 2005; 9(5):220–225. DOI: 10.1016/j.tics.2005.03.003 [PubMed: 15866148]
- Hernandez AE, Martinez A, Kohnert K. In search of the language switch: An fMRI study of picture naming in Spanish–English bilinguals. *Brain and Language*. 2000; 73(3):421–431. DOI: 10.1006/brln.1999.2278 [PubMed: 10860563]
- Higgins R. French, English, and the idea of gay language in Montreal. In: Boellstorff T, Leap W, editors *Speaking in queer tongues: Globalization and gay language*. Urbana and Chicago: University of Illinois Press; 2004. 72–104.
- Hofweber J, Marinis T, Treffers-Daller J. Effects of dense code-switching on executive control. *Linguistic Approaches to Bilingualism*. 2016; 6:648–668. DOI: 10.1075/lab.15052.hof
- Hopp H. Cross-linguistic lexical and syntactic co-activation in L2 sentence processing. *Linguistic Approaches to Bilingualism*. 2016; 7(1):96–130. DOI: 10.1075/lab.14027.hop
- Just MA, Carpenter PA. A capacity theory of comprehension: Individual differences in working memory. *Psychological Review*. 1992; 99(1):122–149. DOI: 10.1037/0033-295X.99.1.122 [PubMed: 1546114]
- Jyväskylä J, Soveri A, Wahlström J, Lehtonen M, Rodriguez-Fornells A, Laine M. Relationship between language switching experience and executive functions in bilinguals: An Internet-based study. *Journal of Cognitive Psychology*. 2017; 29:404–419.
- Kam JWY, Dominelli R, Carlson SR. Differential relationships between sub-traits of BIS-11 impulsivity and executive processes: An ERP study. *International Journal of Psychophysiology*. 2012; 85:174–187. [PubMed: 22659220]
- Kapa LL, Colombo J. Attentional control in early and later bilingual children. *Cognitive Development*. 2013; 28(3):233–246. DOI: 10.1016/j.cogdev.2013.01.011 [PubMed: 24910499]
- Klein D, Mok K, Chen JK, Watkins KE. Age of language learning shapes brain structure: a cortical thickness study of bilingual and monolingual individuals. *Brain and Language*. 2014; 131:20–24. DOI: 10.1016/j.bandl.2013.05.014 [PubMed: 23819901]
- Klein D, Zatorre RJ, Milner B, Meyer E, Evans AC. Left putaminal activation when speaking a second language: evidence from PET. *NeuroReport*. 1994; 5(17):2295. [PubMed: 7881049]
- Kootstra GJ, van Hell JG, Dijkstra T. Syntactic alignment and shared word order in code-switched sentence production: Evidence from bilingual monologue and dialogue. *Journal of Memory and Language*. 2010; 63(2):210–231. DOI: 10.1016/j.jml.2010.03.006
- Kootstra GJ, van Hell JG, Dijkstra T. Priming of code-switches in sentences: The role of lexical repetition, cognates, and language proficiency. *Bilingualism: Language and Cognition*. 2012; 15(04):797–819. DOI: 10.1017/S136672891100068X
- Kousaie S, Chai XJ, Sander KM, Klein D. Simultaneous learning of two languages from birth positively impacts intrinsic functional connectivity and cognitive control. *Brain and cognition*. 2017; 117:49–56. [PubMed: 28648285]
- Kroff JRV, Dussias PE, Gerfen C, Perrotti L, Bajo MT. Experience with code-switching modulates the use of grammatical gender during sentence processing. *Linguistic Approaches to Bilingualism*. 2016; 7(2):163–198.
- Kroll JF, Bobb SC, Misra M, Guo T. Language selection in bilingual speech: Evidence for inhibitory processes. *Acta Psychologica*. 2008; 128(3):416–430. DOI: 10.1016/j.actpsy.2008.02.001 [PubMed: 18358449]
- Kroll JF, Dussias PE, Bogulski CA, Valdes Kroff JR. Juggling two languages in one mind: What bilinguals tell us about language processing and its consequences for cognition. *Psychology of Learning and Motivation: Advances in Research and Theory*. 2012; 56:229–262. DOI: 10.1016/B978-0-12-394393-4.00007-8
- Kroll JF, Gullifer JW, Rossi E. The multilingual lexicon: The cognitive and neural basis of lexical comprehension and production in two or more languages. In: Polio C, editor *Annual Review of Applied Linguistics*. Vol. 33. Cambridge, UK: Cambridge University Press; 2013. 102–127.
- Kuznetsova A, Brockhoff PB, Christensen RHB. *lmerTest: Tests in Linear Mixed Effects Models*. 2016

- Levy BJ, McVeigh ND, Marful A, Anderson MC. Inhibiting your native language: the role of retrieval-induced forgetting during second-language acquisition. *Psychological Science*. 2007; 18(1):29–34. DOI: 10.1111/j.1467-9280.2007.01844.x [PubMed: 17362374]
- Li en M, Hartmann F, Repovš G, Slapničar S. The Impact of Social Pressure and Monetary Incentive on Cognitive Control. *Frontiers in Psychology*. 2016; 7:14–16. [PubMed: 26869945]
- Linck JA, Kroll JF, Sunderman G. Losing access to the native language while immersed in a second language: evidence for the role of inhibition in second-language learning. *Psychological Science*. 2009; 20(12):1507–1515. DOI: 10.1111/j.1467-9280.2009.02480.x [PubMed: 19906121]
- Lipski JM. Code-switching and the problem of bilingual competence. *Aspects of Bilingualism*. 1978:250–264.
- Lipski J. *Linguistic aspects of Spanish-English language switching*. Phoenix, Arizona: Arizona State University; 1985.
- Locke HS, Braver TS. Motivational influences on cognitive control: Behavior, brain activation, and individual differences. *Cognitive, Affective & Behavioral Neuroscience*. 2008; 8(1):99–112. DOI: 10.3758/CABN.8.1.99
- Luk G, Bialystok E, Craik FIM, Grady CL. Lifelong bilingualism maintains white matter integrity in older adults. *The Journal of Neuroscience*. 2011; 31(46):16808–16813. DOI: 10.1523/JNEUROSCI.4563-11.2011 [PubMed: 22090506]
- Luk G, De Sa E, Bialystok E. Is there a relation between onset age of bilingualism and enhancement of cognitive control? *Bilingualism: Language and Cognition*. 2011; 14(04):588–595.
- Luk G, Green DW, Abutalebi J, Grady C. Cognitive control for language switching in bilinguals: A quantitative meta-analysis of functional neuroimaging studies. *Language and Cognitive Processes*. 2012; 27(10):1479–1488. DOI: 10.1080/01690965.2011.613209
- Macizo P, Bajo T, Martín MC. Inhibitory processes in bilingual language comprehension: Evidence from Spanish–English interlexical homographs. *Journal of Memory and Language*. 2010; 63(2):232–244. DOI: 10.1016/j.jml.2010.04.002
- Mechelli A, Crinion JT, Noppeney U, O’Doherty J, Ashburner J, Frackowiak RS, Price CJ. *Neurolinguistics: Structural plasticity in the bilingual brain*. *Nature*. 2004; 431(7010):757–757. DOI: 10.1038/431757a [PubMed: 15483594]
- Meuter RFI, Allport A. Bilingual language switching in naming: Asymmetrical costs of language selection. *Journal of Memory and Language*. 1999; 40(1):25–40. DOI: 10.1006/jmla.1998.2602
- Morales J, Gómez-Ariza CJ, Bajo MT. Dual mechanisms of cognitive control in bilinguals and monolinguals. *Journal of Cognitive Psychology*. 2013; 25(5):531–546. DOI: 10.1080/20445911.2013.807812
- Morales L, Paolieri D, Dussias PE, Valdés Kroff JR, Gerfen C, Bajo MT. The gender congruency effect during bilingual spoken-word recognition. *Bilingualism: Language and Cognition*. 2016; 19(2):294–310. DOI: 10.1017/S1366728915000176
- Murphy K, Birm RM, Handwerker DA, Jones TB, Bandettini PA. The impact of global signal regression on resting state correlations: Are anti-correlated networks introduced? *NeuroImage*. 2009; 44(3):893–905. DOI: 10.1016/j.neuroimage.2008.09.036 [PubMed: 18976716]
- Myers-Scotton C. *Dueling Languages: Grammatical Structure in Code-switching*. Oxford, UK: Clarendon; 1993.
- Novick JM, Trueswell JC, Thompson-Schill SL. Cognitive control and parsing: Reexamining the role of Broca’s area in sentence comprehension. *Cognitive, Affective & Behavioral Neuroscience*. 2005; 5(3):263–281. DOI: 10.3758/CABN.5.3.263
- Olson DJ. Bilingual language switching and selection at the phonetic level: Asymmetrical transfer in VOT production. *Journal of Phonetics*. 2013; 41(6):407–420. DOI: 10.1016/j.wocn.2013.07.005
- Paap KR, Greenberg ZI. There is no coherent evidence for a bilingual advantage in executive processing. *Cognitive Psychology*. 2013; 66(2):232–258. DOI: 10.1016/j.cogpsych.2012.12.002 [PubMed: 23370226]
- Pelham SD, Abrams L. Cognitive advantages and disadvantages in early and late bilinguals. *Journal of Experimental Psychology: Learning, Memory, and Cognition*. 2014; 40(2):313. doi: 10.1037/a0035224

- Peretz Y, Lavidor M. Enhancing lexical ambiguity resolution by brain polarization of the right posterior superior temporal sulcus. *Cortex*. 2013; 49(4):1056–1062. DOI: 10.1016/j.cortex.2012.03.015 [PubMed: 22513342]
- Pillai JJ, Araque JM, Allison JD, Sethuraman S, Loring DW, Thiruvaiyaru D, et al. Functional MRI study of semantic and phonological language processing in bilingual subjects: preliminary findings. *NeuroImage*. 2003; 19(3):565–576. DOI: 10.1016/S1053-8119(03)00151-4 [PubMed: 12880788]
- Pivneva I, Mercier J, Titone D. Executive control modulates cross-language lexical activation during L2 reading: evidence from eye movements. *Journal of Experimental Psychology: Learning, Memory, and Cognition*. 2014; 40(3):787–796. DOI: 10.1037/a0035583
- Pliatsikas C, Moschopoulou E, Saddy JD. The effects of bilingualism on the white matter structure of the brain. *Proceedings of the National Academy of Sciences of the United States of America*. 2015; 112(5):1334–1337. DOI: 10.1073/pnas.1414183112 [PubMed: 25583505]
- Poplack S. Sometimes I'll start a sentence in Spanish y termino en español: Toward a typology of code-switching. *Linguistics*. 1980; 18:581–618.
- Price CJ. The anatomy of language: A review of 100 fMRI studies published in 2009. *Annals of the New York Academy of Sciences*. 2010; 1191(1):62–88. DOI: 10.1111/j.1749-6632.2010.05444.x [PubMed: 20392276]
- Prior A, Gollan TH. Good language-switchers are good task-switchers: Evidence from Spanish-English and Mandarin-English bilinguals. *Journal of the International Neuropsychological Society*. 2011; 17:682–691. [PubMed: 22882810]
- Prior A, MacWhinney B. A bilingual advantage in task switching. *Bilingualism: Language and Cognition*. 2010; 13(02):253–262. DOI: 10.1017/S1366728909990526
- R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing; Vienna, Austria: 2017. <http://www.R-project.org/>
- Rodriguez-Fornells A, van Der Lugt A, Rotte M, Britti B, Heinze HJ, Münte TF. Second language interferes with word production in fluent bilinguals: Brain potential and functional imaging evidence. *Journal of Cognitive Neuroscience*. 2005; 17(3):422–433. [PubMed: 15814002]
- Rogers RD, Monsell S. Costs of a predictable switch between simple cognitive tasks. *Journal of Experimental Psychology: General*. 1995; 124(2):207–231. DOI: 10.1037/0096-3445.124.2.207
- Rosvold HE, Mirsky AF, Sarason I, Bransome EDJ, Beck LH. A continuous performance test of brain damage. *Journal of Consulting Psychology*. 1956; 20(5):343–350. DOI: 10.1037/h0043220 [PubMed: 13367264]
- Saad ZS, Gotts SJ, Murphy K, Chen G, Jo HJ, Martin A, Cox RW. Trouble at rest: how correlation patterns and group differences become distorted after global signal regression. *Brain Connectivity*. 2012; 2(1):25–32. [PubMed: 22432927]
- Shannon CE. A mathematical theory of communication. *Bell System Technical Journal*. 1948; 27:379–423.
- Shapleske J, Rossell SL, Woodruff PW, David AS. The planum temporale: a systematic, quantitative review of its structural, functional and clinical significance. *Brain Research Brain Research Reviews*. 1999; 29(1):26–49. <http://>. DOI: 10.1016/S0165-0173(98)00047-2 [PubMed: 9974150]
- Simon JR, Berbaum K. Effect of conflicting cues on information processing: The 'Stroop effect' vs. the 'Simon effect'. *Acta Psychologica*. 1990; 73(2):159–170. DOI: 10.1016/0001-6918(90)90077-S [PubMed: 2343770]
- Soveri A, Rodriguez-Fornells A, Laine M. Is there a relationship between language switching and executive functions in bilingualism? Introducing a within group analysis approach. *Frontiers in Psychology*. 2011; 2:1–8. [PubMed: 21713130]
- Stroop JR. Studies of interference in serial verbal reactions. *Journal of Experimental Psychology*. 1935; 18(6):643–662. DOI: 10.1037/h0054651
- Tao L, Marzecová A, Taft M, Asanowicz D, Wodniecka Z. The efficiency of attentional networks in early and late bilinguals: The role of age of acquisition. *Frontiers in Psychology*. 2011; 2doi: 10.3389/fpsyg.2011.00123

- Thompson-Schill SL, D'Esposito M, Aguirre GK, Farah MJ. Role of left inferior prefrontal cortex in retrieval of semantic knowledge: A reevaluation. *Proceedings of the National Academy of Sciences*. 1997; 94(26):14792–14797. DOI: 10.1073/pnas.94.26.14792
- Thompson-Schill SL, D'Esposito M, Kan IP. Effects of repetition and competition on activity in left prefrontal cortex during word generation. *Neuron*. 1999; 23(3):513–522. DOI: 10.1016/S0896-6273(00)80804-1 [PubMed: 10433263]
- Titone D, Gullifer J, Subramaniapillai S, Rajah N, Baum S. History-inspired reflections on the bilingual advantages hypothesis. In: Bialystok E, editor *Growing old with two languages: Effects of bilingualism on cognitive aging*. Amsterdam, The Netherlands: John Benjamins; 2017.
- Ullman MT. Contributions of memory circuits to language: the declarative/procedural model. *Cognition*. 2004; 92(1-2):231–270. DOI: 10.1016/j.cognition.2003.10.008 [PubMed: 15037131]
- Ullsperger M, King JA. Proactive and reactive recruitment of cognitive control: Comment on Hikosaka and Isoda. *Trends in Cognitive Sciences*. 2010; 14:191–192. [PubMed: 20363177]
- van Heuven WJB, Schriefers H, Dijkstra T, Hagoort P. Language conflict in the bilingual brain. *Cerebral Cortex*. 2008; 18(11):2706–2716. DOI: 10.1093/cercor/bhn030 [PubMed: 18424776]
- Verreyt N, Woumans E, Vandelanotte D, Szmalec A, Duyck W. The influence of language-switching experience on the bilingual executive control advantage. *Bilingualism: Language and Cognition*. 2016; 19(1):181–190.
- Wartenburger I, Heekeren HR, Abutalebi J, Cappa SF, Villringer A, Perani D. Early setting of grammatical processing in the bilingual brain. *Neuron*. 2003; 37:159–170. [PubMed: 12526781]
- Whitfield-Gabrieli S, Nieto-Castanon A. Conn: a functional connectivity toolbox for correlated and anticorrelated brain networks. *Brain Connectivity*. 2012; 2(3):125–141. [PubMed: 22642651]
- Whitford V, Pivneva I, Titone D. *Methods in Bilingual Reading Comprehension Research*. New York, NY: Springer; 2016. Eye movement methods to investigate bilingual reading; 183–211.
- Whitford V, Titone D. Second-language experience modulates first- and second-language word frequency effects: evidence from eye movement measures of natural paragraph reading. *Psychonomic Bulletin & Review*. 2012; 19(1):73–80. DOI: 10.3758/s13423-011-0179-5 [PubMed: 22042632]
- Zhang H, Kang C, Wu Y, Ma F, Guo T. Improving proactive control with training on language switching in bilinguals. *NeuroReport*. 2015; 26(6):354–359. DOI: 10.1097/WNR.0000000000000353 [PubMed: 25756906]
- Zirnstein M, van Hell JG, Kroll JF. Cognitive control ability mediates prediction costs in monolinguals and bilinguals. *Cognition*. 2018; 176:87–106. [PubMed: 29549762]

Highlights

- Bilingual experience adaptively tunes neural networks involved in executive control
- Early L2 AoA relates to greater frontal interhemispheric functional connectivity
- Greater diversity of language use relates to greater subcortical connectivity
- Frontal and subcortical connectivity relate to proactive-reactive shifts in behavior
- Historical and ongoing language experience impact functional brain connectivity

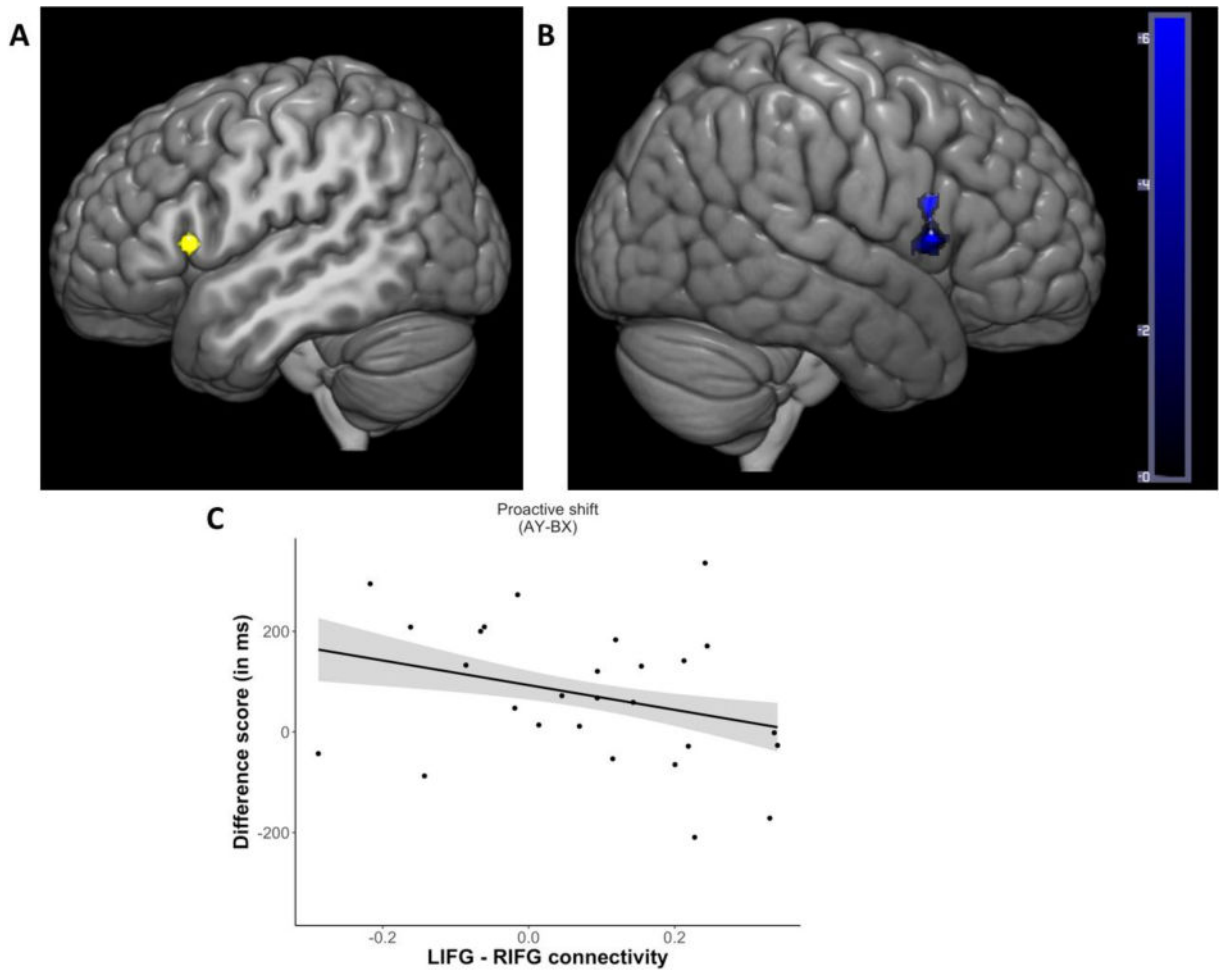


Figure 1. Connectivity between the LIFG seed (yellow) and RIFG (blue) correlated with L2 AoA. **A**, Left hemisphere view indicating the location of the LIFG BA 44 seed. **B**, Right hemisphere view indicating the RIFG cluster (scale depicts t -statistics) that showed a significant negative relationship between connectivity strength and L2 AoA. **C**, Association between connectivity (Fisher's z) and performance on the AX-CPT: greater LIFG – RIFG connectivity was associated with a shift away from proactive control strategies (i.e., smaller speed advantages for BX relative to AY trials).

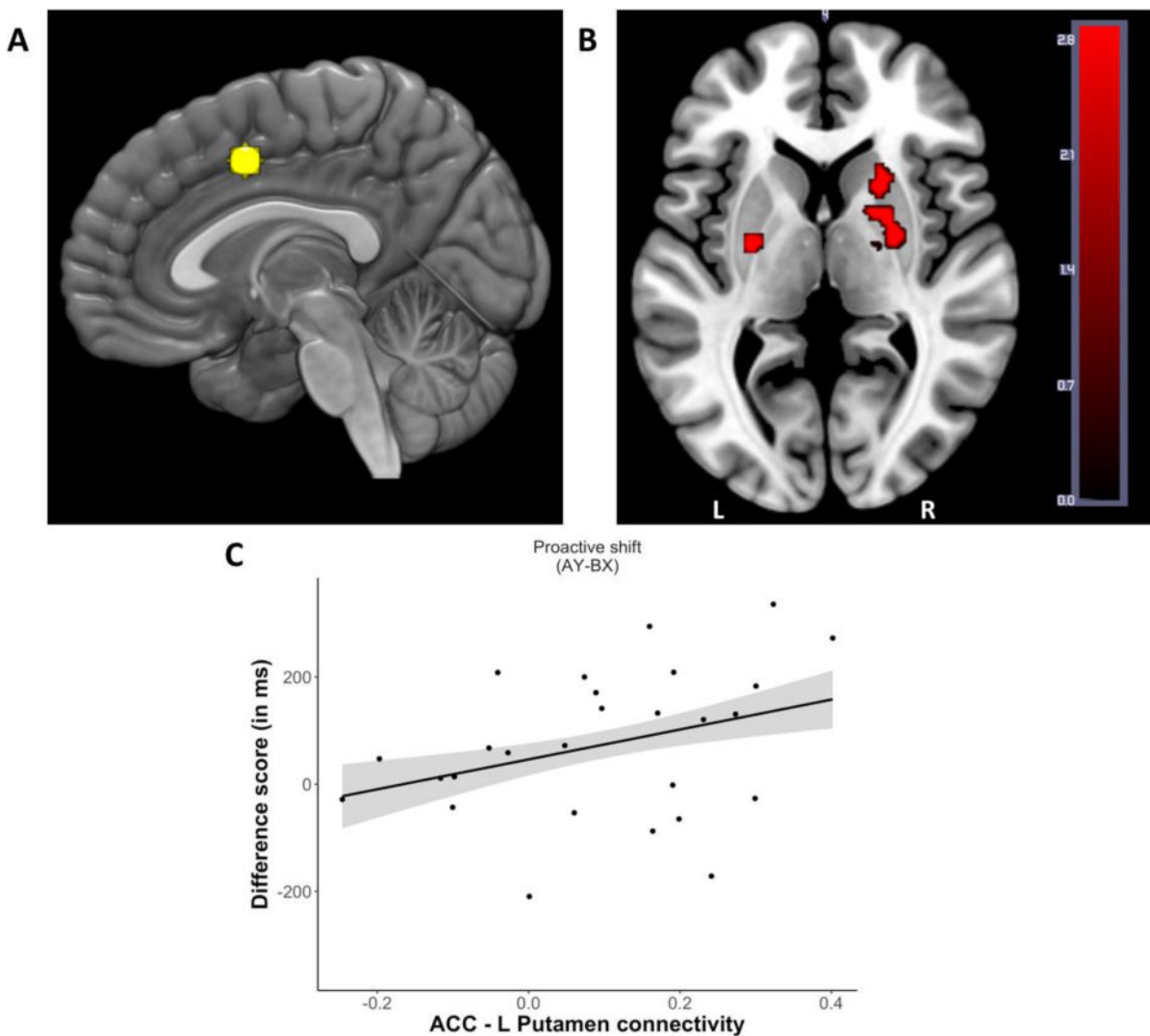


Figure 2. Connectivity between the ACC (yellow) and putamen bilaterally (red) correlated with language entropy. **A**, Medial view of the right hemisphere indicating the location of the ACC seed. **B**, Superior view indicating clusters (scale depicts t -statistics) in left and right putamen that showed significant positive relationships between connectivity strength and language entropy. **C**, Association between connectivity (Fisher's z) and performance on the AX-CPT: ACC-putamen connectivity was associated with a shift towards proactive control strategies (i.e., greater speed advantages for BX relative to AY trials).

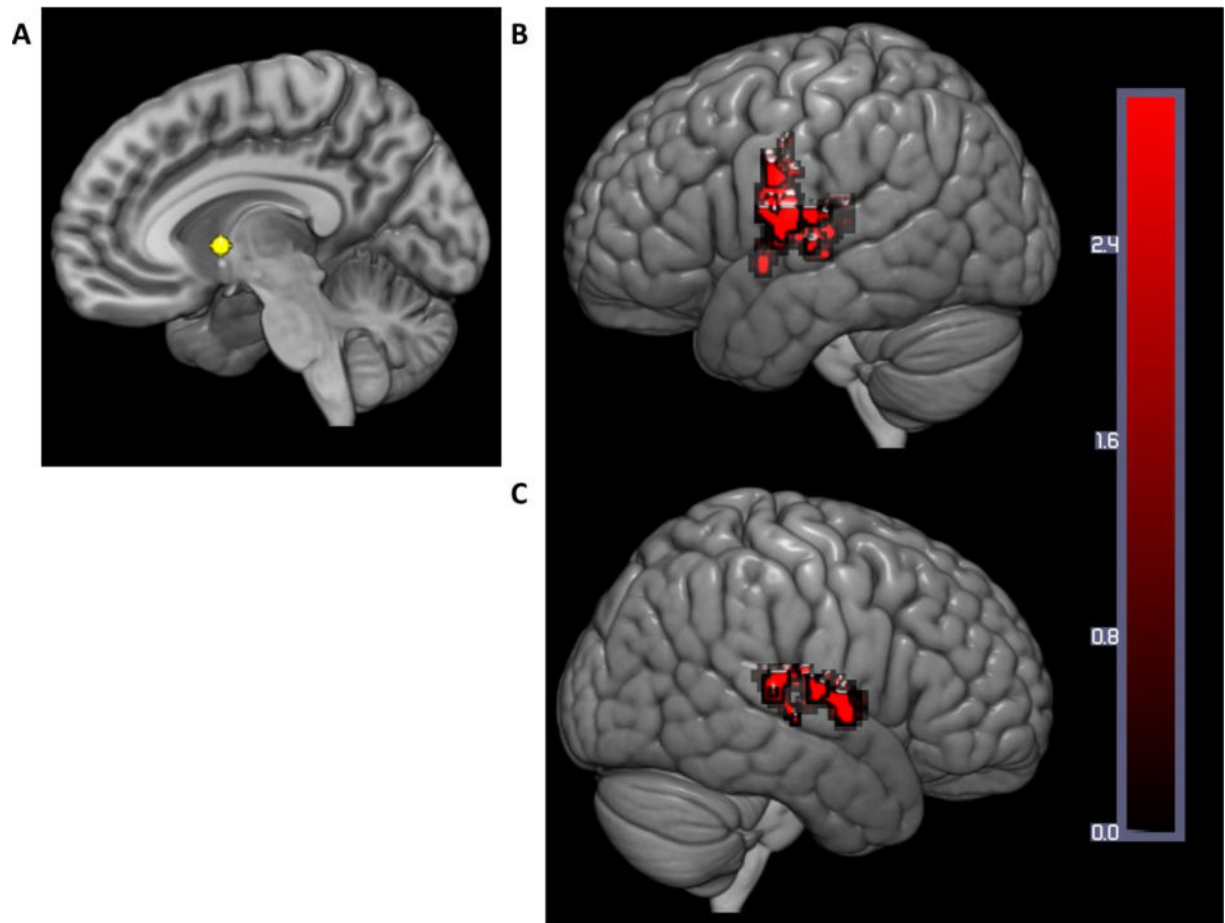


Figure 3. Connectivity between the left caudate (yellow) and STG (red) bilaterally correlated with language entropy. **A**, Left hemisphere view indicating the location of the left caudate seed. **B**, Left hemisphere view indicating the left STG cluster that showed a significant positive relationship between connectivity strength and language entropy. **C**, Right hemisphere view indicating the right STG cluster that showed a significant positive relationship between connectivity strength and language entropy. The scale depicts t -statistics.

Table 1

Regions of interest (ROI)

ROI	x	y	z
Anterior Cingulate (BA 24)	0	+06	+44
Left Caudate	-08	+04	+02
Left Inferior Frontal Gyrus (BA 44)	-50	+18	+06
Left Inferior Frontal Gyrus (BA 47)	-32	+20	-08
Left Inferior Parietal Lobule (BA 40)	-54	-34	+36

Seed regions consisted of 6 mm spheres. Coordinates are represented in MNI Space.

Table 2

Significant clusters for L2 AoA controlling for language entropy

ROI seeds	Direction	Cluster size	Peak (MMNI)			p-FDR	Cluster location
			x	y	z		
LIFG (BA44)	-	84	-58	+12	+24	0.014182	LIFG pars opercularis
	-	164	+56	+16	+06	0.000409	RIFG pars opercularis
	-	55	-40	+46	+24	0.040743	L frontal pole
	-	66	-56	-02	-40	0.030570	L ITG
	-	56	-66	-44	+32	0.040743	L SMG
	-	163	+60	-30	+34	0.000409	R SMG
	+	102	-08	-18	+70	0.005132	L precentral gyrus
	+	372	-06	-26	+64	< 0.000001	L/R precentral gyrus
	+	161	-34	-26	+44	0.000578	L pre/postcentral gyrus
	+	127	+46	-14	+64	0.001915	R pre/postcentral gyrus
	+	67	+38	-16	+44	0.029646	R precentral gyrus
	+	61	+32	-28	+66	0.035790	R pre/postcentral gyrus
	+	58	-58	-14	+04	0.037092	L STG
LIFG (BA 47)							
ACC (BA 24)							
Left Caudate							
L IPL (BA 40)	-	221	0	+26	+66	0.000094	L/R SFG

Peak voxel-level significance is set at $p < 0.001$, uncorrected. Direction indicates whether the correlation between L2 AoA and connectivity is positive or negative.

Table 3

Significant clusters for language entropy controlling for AoA

ROI seeds	Direction	Cluster size	Peak (MNI)			p-FDR	Cluster location
			x	y	z		
LIFG (BA44)	-	117	+22	+72	+04	0.003247	R frontal pole
	-	69	-58	-02	-40	0.017509	L MTG/ITG
	+	99	+36	-16	+44	0.025153	R precentral gyrus
LIFG (BA47)							
ACC (BA24)	-	85	+06	-74	+60	0.035534	Precuneous
	+	107	-26	-08	+04	0.005022	L putamen
Left Caudate	+	250	+26	-04	+00	0.000023	R putamen
	+	837	-58	-02	+30	< 0.000001	L STG
LIPL (BA 40)	+	491	+56	+00	+02	< 0.000001	R STG
	+	143	-26	-42	+68	0.000457	L postcentral gyrus/SPL
LIPL (BA 40)	+	91	+24	-36	+64	0.004730	R postcentral gyrus/SPL
	+	100	-58	-20	+48	0.003495	L postcentral gyrus
LIPL (BA 40)	+	83	+52	-06	+50	0.006383	R pre/postcentral

Peak voxel-level significance is set at $p < 0.001$, uncorrected. Direction indicates whether the correlation between mean language entropy and connectivity is positive or negative.

Table 4

Fixed effects of the linear mixed effects model on AX-CPT data

Effect	Estimate	Std. Error	<i>t</i> value
(Intercept = Condition <i>AY</i>)	6.20	0.04	158.83*
Condition <i>BY</i>	-0.33	0.03	-12.99*
Condition <i>AX</i>	-0.41	0.02	-20.92*
Condition <i>BX</i>	-0.28	0.03	-10.96*
LIFG-RIFG connectivity	-0.03	0.04	-0.81
ACC- L Putamen connectivity	0.06	0.06	1.00
ACC- R Putamen connectivity	-0.05	0.06	-0.76
Condition <i>BY</i> * LIFG-RIFG connectivity	0.09	0.03	3.44*
Condition <i>AX</i> * LIFG-RIFG connectivity	0.07	0.02	3.16*
Condition <i>BX</i> * LIFG-RIFG connectivity	0.16	0.03	6.00*
Condition <i>BY</i> * ACC-L putamen connectivity	-0.03	0.04	-0.75
Condition <i>AX</i> * ACC-L putamen connectivity	-0.10	0.03	-2.94*
Condition <i>BX</i> * ACC-L putamen connectivity	-0.10	0.04	-2.27*
Condition <i>BY</i> * ACC-R putamen connectivity	-0.03	0.04	-0.82
Condition <i>AX</i> * ACC-R putamen connectivity	0.01	0.03	0.33
Condition <i>BX</i> * ACC-R putamen connectivity	-0.04	0.04	-0.90

The intercept represents the *AY* control condition. Numeric predictors (i.e., connectivity values) are centered and scaled. Asterisks indicate significance.