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The bilingual language network: Differential involvement of anterior cingulate, basal ganglia and prefrontal cortex in preparation, monitoring, and execution



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ABSTRACT

Research on the neural bases of bilingual language control has largely overlooked the role of preparatory processes, which are central to cognitive control. Additionally, little is known about how the processes involved in global language selection may differ from those involved in the selection of words and morpho-syntactic rules for manipulating them. These processes were examined separately in an fMRI experiment, with an emphasis on understanding how and when general cognitive control regions become activated. Results of region-of-interest analyses on 23 early Spanish-English bilinguals showed that the anterior cingulate cortex (ACC) was primarily engaged during the language preparation phase of the task, whereas the left prefrontal (DLPFC) and presupplementary motor areas showed increasing activation from preparation to execution. Activation in the basal ganglia (BG), left middle temporal lobe, and right precentral cortical regions did not significantly differ throughout the task. These results suggest that three core cognitive control regions, the ACC, DLPFC, and BG, which have been previously implicated in bilingual language control, engage in distinct neurocognitive processes. Specifically, the results are consistent with the view that the BG "keep track" of the target language in use throughout various levels of language selection, that the ACC is particularly important for top-down target language preparation, and that the left prefrontal cortex is increasingly involved in selection processes from preparation through task execution.

Introduction

Bilingual language control refers to the set of mechanisms used for the selection and maintenance of a target language in the face of competing symbolic word representations and morpho-syntactic rules for manipulating them (Costa et al., 1999; Hatzidaki et al., 2011). Such control is likely underpinned by multiple processes, including the selection of the language to use at a given situation, the generation of linguistic goals (e.g., pluralizing a word based on the target language) and the selection of word forms and rules for manipulating words to achieve the goal (e.g., Guo et al., 2011; Branzi et al., 2015; Hoversten et al., 2015). As a result, bilingual language control likely involves multiple sub-component neurocomputations deployed across various situations (e.g., speaking a foreign language continuously while abroad vs. translating between individuals) and applied to different levels of selection (e.g., the need to

speak in the Spanish language vs. the need to conjugate the verb "hablar" in Spanish). Many of these intricacies are yet to be addressed in the bilingual language control literature. The current study aims to advance understanding of the neurocognitive mechanisms of bilingual language control.

The role of general control mechanisms in bilingualism

The existing body of literature investigating the neural underpinnings of bilingual language use has widely implicated three regions known to be more broadly involved in cognitive control: the dorsolateral prefrontal cortex (DLPFC), the basal ganglia (BG), and the anterior cingulate cortex (ACC). In the first fMRI investigation of bilingual language switching, Hernandez et al. (2000) used a picture-naming paradigm in which the target language either switched between Spanish and English or

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remained stable in either language within a block. The results showed that activation in the left DLPFC increased in the switching condition where competition for selection between two available languages became maximized. In a series of follow-up studies, Hernandez and colleagues replicated and extended their original findings, showing repeatedly that the DLPFC is specifically engaged when bilinguals are asked to switch between target languages as opposed to maintaining a particular language (Hernandez et al., 2001; Hernandez, 2009). This is consistent with the broad body of literature implicating the DLPFC in cognitive control. Specifically, when tasks involve response conflict of some kind (e.g., Mansouri et al., 2009) the DLPFC is involved in goal maintenance or storing a set of rules for behaving given specific conditions (Miller and Cohen, 2001; Wallis et al., 2001; Cole et al., 2010; Becker et al., 2016).

In parallel, evidence from neuropsychological (e.g., Abutalebi et al., 2000; Fabbro, 2001), neurosurgical (Robles et al., 2005), and neuro-imaging (e.g., Crinion et al., 2006; Lehtonen et al., 2005) studies has implicated the BG, and particularly the caudate nucleus, in bilingual language control. The BG are a set of subcortical nuclei composed of the subthalamic nucleus, the substantia nigra, the external and internal segments of the globus pallidus, and the striatum. The striatum consists of the caudate and putamen, and serves as the input station of the circuit. The BG receive inputs from the entire cortex and modulate signals to prefrontal regions (including both DLPFC and ACC) in a manner well-suited for dynamically reprioritizing responses (e.g., Stocco et al., 2014; Stocco et al., 2010).

Importantly for cognitive control, the BG are rich in dopamine, and thus have been associated with cognitive flexibility more so than the DLPFC (Pasupathy and Miller, 2005). Based on modeling work demonstrating "Conditional Routing" of signals to the prefrontal cortex through the BG (Stocco et al., 2010), Stocco et al. (2010) proposed a shared role for the BG, and the striatal nuclei in particular, in bilingual language control. According to the model, the BG actively mediate signaling to the prefrontal cortex according to the dynamically changing target language being used by a bilingual at any given time.

In their theoretical review paper, Abutalebi and Green (2007) discuss research on bilingual language production under the lens of general cognitive control mechanisms. This review and subsequent refinements from the group (Green and Abutalebi, 2013; Abutalebi and Green, 2016) included an important role for the ACC, which is generally characterized as a region that detects or monitors conflict (e.g., Botvinick et al., 1999; Kerns et al., 2004), as well as for the DLPFC and BG. Specifically, they proposed that controlled language production in bilingual individuals involves the dynamic interplay between conflict monitoring in the ACC, executive functioning (including response selection and inhibition) in the DLPFC, language planning, selection, and switching executed by the BG, and maintenance of representations in working memory in the parietal lobe. In a subsequent neuroimaging investigation, Abutalebi and colleagues confirmed that the ACC and BG were involved in monitoring target language during a bilingual picture-naming task (Abutalebi et al., 2007). They continued to demonstrate that consistent conflict monitoring in bilingual individuals shapes the ACC both structurally and functionally in a way that gives rise to more efficient processing of conflict in non-linguistic tasks as well (Abutalebi et al., 2011).

In summary, research on the neural basis of bilingualism has repeatedly implicated the DLPFC, BG, and ACC in bilingual language control. The goal of the current study was to understand the role of bilingual language control regions in different phases of bilingual language control processing.

The role of proactive control in bilingualism

Cognitive control research has identified two classes of control mechanisms: *Proactive control*, which is deployed early, and typically makes use of predictive cues to guide information processing in a top-down and goal-oriented manner; and *reactive control*, which is largely

driven by bottom-up processes that trigger a corrective function following unanticipated detection of conflict (e.g., Braver et al., 2007; Braver, 2012). The role of proactive control in bilingual language use has been largely ignored. For example, in a recent meta-analysis of the neural networks supporting bilingual language control (Luk et al., 2012), none of the ten experiments employed paradigms in which language preparation could be investigated separately from language use. Interestingly, this meta-analysis did not find significant activation in the ACC across experiments. In the real world, however, bilinguals likely use predictive cues about which language they should speak, whether it be broad contextual cues such as the location (e.g., at home versus at work), previous experience with the individual they are speaking to, or more subtle (and certainly less predictable) cues such as the ethnicity of a person they are about to interact with.

One recent experiment by Woumans et al. (2015) investigated the cognitive effect of preparatory processes on bilingual language control by training participants with faces that were reliably associated with particular language profiles. Each face was presented 2,000 milliseconds before a speech event. Certain faces were reliably followed by speech in one language, while other "bilingual" faces were followed by speech in two languages. When given a noun in either language, participants were able to more rapidly produce associated verbs when a familiar face, regularly associated with speech in one particular language, served as the preparatory cue for a trial. In contrast, participants experienced more difficulty with the task when either an unfamiliar face, or a familiar bilingual face preceded the trial. These results are consistent with research on general cognitive control which has shown that predictive cues enable proactive adjustment for the desired subsequent task (Braver, 2012; Sohn and Carlson, 2000; Ruge et al., 2013; Zhang et al., 2013).

To the best of our knowledge, only one neuroimaging investigation to date has measured the role of preparatory cuing in bilingual language control. Reverberi et al. (2015) presented an abstract cue indicating "target language" in advance of a to-be-named picture. They found that language switching during preparation resulted in activation in the left middle temporal gyrus, right parietal lobe, and bilateral precuneus. In contrast, during task execution, the medial prefrontal cortex was more highly activated when target language switched than when it was repeated. Thus, when task preparation and execution were separately examined in a naming task, different sets of regions were implicated in different phases. The current paper aims to extend the existing research by investigating the neural mechanisms associated with preparatory cuing during a novel bilingual language task.

Investigating morpho-syntactic rule application in bilinguals

A second limitation of the existing bilingual control literature is that the majority of it has been limited to lexico-semantic selection processes, most commonly operationalized through picture-naming or picture-word-matching tasks. While lexical selection in the face of competing representations is clearly one of the demands placed on a bilingual language control system, such selection also occurs in morpho-syntactic processing. To the best of our knowledge, none of the switching paradigms typically used to study bilingual language control has included morpho-syntactic manipulations. This is important to consider, however, as research has shown that co-activation of linguistic information in the bilingual brain is not limited to the lexico-semantic level (Pickering and Ferreira, 2008; Hatzidaki et al., 2011). Intersentential codeswitching and cross-linguistic structural priming provide additional evidence that the need to manage interference between languages extends to morpho-syntactic levels (Pickering and Ferreira, 2008).

Separating control processes from stimulus-driven associations

A third, but less pervasive, limitation of the existing bilingual control literature is that it is difficult to separate top-down linguistic control processes from any bottom-up influences that are driven by stimuli

occurring in a particular language. It is likely that hearing or reading a word in a particular language will prime other related words in the same language and the rules for manipulating words in that particular language. Often in bilingual language control experiments, the target language itself is used to indicate which language a particular task should be executed in. For example, in their seminal bilingual language switching investigation, Hernandez et al. (2001) used the words "say" and "diga" presented simultaneously with a picture to instruct participants which language to name an object in. Similarly, in a Chinese-English switching task, Wang et al. (2009) used either a Chinese character "读" or the English counterpart 'read' to indicate which language a trial should be executed in. In the real world, bilingual language control, like any other cognitive control, involves dynamic interactions between top-down planning and attention allocation and bottom-up, stimulus driven biasing of information. However, including both types of information in a paradigm makes it complicated to understand what is driving behavior and brain activation. Therefore, the current paradigm uses non-linguistic, symbolic cues to attempt to isolate stimulus-driven effects from preparatory processes.

Rapid Instructed Task Learning paradigm

The current paper addresses these three limitations through the development of a novel paradigm that allows: (1) the separation of preparatory processes from task execution, (2) the investigation of bilinguals' morpho-syntactic rule selection and application, and (3) the separation of top-down control structures from bottom-up linguistic influences. Specifically, we employed a variant of the Rapid Instructed Task Learning (RITL) paradigm, which is gaining popularity as a tool for understanding how the human brain executes rule-based behaviors (Stocco et al. 2012; Cole et al. 2013; Stocco and Prat, 2014). One critical feature of the RITL paradigm is that the rules for completing a subsequent task are presented before the stimuli on which the rules need to be applied. This allows one to estimate the neural processes involved in dynamically constructing a mental program for controlled behavior separately from the execution of that behavior. In the current experiment, this design feature provides the ability to separate preparation from execution in bilingual language control, and to separate the top-down processes associated with generating a control structure from the bottom-up influences of linguistic stimuli. This separation allows one to investigate the control mechanism(s) that is established to perform a task without influence from the stimuli.

Predictions

Our predictions focus on three questions central to bilingual language control research that can be extracted using this novel research design: (1) How and when do general cognitive control regions participate in bilingual language control? (2) How do the neural networks involved in proactive control differ from those involved in bilingual language production? and (3) How do the neural networks involved in global language selection differ from those involved in morpho-syntactic rule selection?

To address these questions, the analyses conducted herein will be centered primarily upon the regions identified in a quantitative metaanalysis on the neurobiology of bilingual language control (Luk et al.,
2012). Specifically, Luk et al. (2012) identified a network of brain regions that have been consistently reported in investigations of bilingual
language control. This network includes regions discussed herein that are
typically associated more generally with cognitive control including:
DLPFC, BG (specifically bilateral caudate nuclei), and pre-supplementary
motor areas (pre-SMA), also discussed by Abutalebi and Green as part of
the ACC conflict monitoring network (Abutalebi and Green, 2016). Not
surprisingly, the results also included regions more broadly associated
with language processes such as the left inferior frontal gyrus (BA 44, 47)
and the left middle temporal gyrus (BA 37). However, as our task does

vary significantly from those reported in the meta-analysis, we also conducted exploratory, voxelwise, whole-brain analyses.

To address the first question, "How and when do general cognitive control regions participate in bilingual language control?" our primary analyses will investigate how activation changes in these regions of interest, defined a priori based on the meta-analysis, across the three task phases. Based on the Conditional Signal Routing Theory (Stocco et al., 2010; Stocco et al., 2014) and the results of Crinion et al. (2006), we predict that the BG will be consistently involved in tracking the target language throughout the different phases of a single trial. In contrast, we predict that brain activity in the DLPFC will increase as the trial progresses from language preparation to rule execution, due to increases in working memory demands. Finally, we predict that the ACC will be most highly activated during task execution, as it is believed to work in concert with the Pre-SMA and DLPFC to address response conflict (Abutalebi and Green, 2007, 2016; Becker et al., 2016).

To address the second question, "How do the neural networks involved in proactive control differ from those involved in bilingual language production?" we will compare patterns of whole-brain activation during language preparation to those obtained during task execution. Based on the research reported by Reverberi et al. (2015), we predict that posterior regions including the middle temporal gyrus, parietal lobes, and precuneus will be more active during preparation, whereas the medial frontal gyrus and all of the canonical left hemisphere language processing regions (e.g., Broca's area in inferior frontal gyrus and Wernicke's area in superior-posterior temporal gyrus) will be more active during execution, which involves the processing of linguistic stimuli. As previously discussed, we also predict that ACC and DLPFC will be more active during task execution.

Finally, to address the third question, "How do the neural networks involved in global language selection differ from those involved in morpho-syntactic rule selection?" we will compare patterns of whole-brain activation during target language preparation to those obtained during morpho-syntactic rule selection. In their review, Buchweitz and Prat (2013) suggested that linguistic rules are organized hierarchically in the bilingual brain, according to target language. Based on research showing that more abstract rules engage more rostral regions of the PFC (Badre, 2008; Koechlin et al., 2003), Buchweitz and Prat (2013) proposed that target language may be represented more rostrally than morphosyntactic rules. Thus, we predict that both selecting target language and selecting morpho-syntactic rules will recruit the left lateral prefrontal cortex (and in particular the inferior frontal gyrus) but that global target language will recruit more rostral PFC regions.

Materials and methods

Participants

Twenty-four, right handed Spanish-English bilinguals (20 females, aged 18–31 years) were paid for participation in the current study. Participants were required to be highly proficient in both languages (as assessed through grammatical proficiency tests) and to have learned both languages before the age of seven. Bilingual language experience information is summarized in Table 1.

 Table 1

 Language characteristics of bilingual participants with standard deviations in parentheses.

Language Profile Measurement (Raw Score)	Spanish Mean (STDEV)	English Mean (STDEV)
Age of Acquisition	3.09 (2.25)	1.89 (2.29)
Self Rated Speaking Proficiency (10)	7.80 (1.07)	9.43 (0.88)
Self Rated Understanding Proficiency (10)	8.73 (1.17)	9.45 (0.58)
Self Rated Reading Proficiency (10)	7.41 (1.59)	9.43 (0.73)
Tested Grammatical Proficiency (50:	85.30% (3.93)	90.90% (1.56)
Spanish, 20: English)		

All participants were healthy, with no history of developmental or neurological disorders. All participants provided informed consent, consistent with the protocols approved by the University of Washington's Institutional Review Board. Data was removed from one participant due to excessive in-scanner motion, defined as more than 10% of images being removed for $> 1\,\mathrm{mm}$ rigid displacement between consecutive volumes. Data from the remaining 23 participants are reported herein.

Materials

Rapid Instructed Task Learning (RITL) paradigm

In the current experiment, each RITL trial began with a preparatory symbolic cue indicating which language the trial was to be executed in. The neural activity associated with processing of this cue reflects the mechanism for preparing to speak in a target language and using this information to guide subsequent attention to word forms and rules within that particular language. After target language cuing, participants saw a code indicating which morpho-syntactic rule(s) they will be asked to apply. Again, this phase preceded any linguistic stimuli. Thus, neural activation during this phase should reflect the processes involved in selection of competing morpho-syntactic rules. To the best of our knowledge, no experiment to date has compared the processes involved in global, target language preparation from those involved in morphosyntactic rule processing. The final phase of the task involved presentation of a word or a word pair on which the participants then performed the instructed rule. These words were always presented in the target language that was cued at the beginning of the trial (e.g., English). During this phase, participants performed the instructed manipulation (e.g., pluralize) on the stimulus provided (e.g., dog) and subvocally produced the word "dogs." This phase of the current experiment shares the most features with existing bilingual language control research, as task execution in an instructed language is what is typically measured.

The RITL paradigm used in the current experiment consisted of 72 total trials, 36 in English and 36 in Spanish. The total of 72 trials were divided into 4 blocks of 18 trials, and each block contained 9 English and 9 Spanish trials (3 of each rule type), presented in pseudo randomized order. Languages were mixed within blocks and randomly varied from trial to trial. Each trial involved the presentation of information across three phases. The first "Prepare Target Language" phase consisted of a symbolic cue (# or *) which indicated that the next trial would be in either Spanish or English. Mapping between a particular symbol and a particular target language was counter-balanced across participants. The second "Rule Selection" phase of the task involved the presentation of one of three types of morpho-syntactic rules: rules for manipulating nouns (generate pronoun or pluralize), rules for manipulating verbs (conjugate past or future tense) and combined rules which consisted of all pairings of noun-verb manipulations (e.g., pluralize noun and conjugate past tense of verb). All rules were indicated with alphanumeric symbols that remained constant across languages ("1" and "2" for noun rules, and "A" and "B" for verb rules). Each type of rule was presented equally often (24 nouns, 24 verbs, and 24 noun-verb combinations) across the experiment. The third "Execution" phase of the experiment involved the presentation of words in either English or Spanish. The words were always presented in the same language cued by the "Prepare Target Language" instruction. All nouns and verbs chosen were highly frequent (top 5%) using both English and Spanish frequency norms (Wiktionary, 2017a,b), with no significant differences in frequency between Spanish and English words (p = 0.82). They also all had regular conjugations. To best equate morphosyntactic processes across languages, nouns used for the pronoun rule had biological gender in both languages (e.g., grandmother, aunt). No word was presented in both its English and Spanish forms within participants, however all words occurred in both languages across stimulus lists, which were counterbalanced across participants. At the end of each trial, participants saw a "Response Verification Probe" which consisted of a word or word combinations that could be produced by applying the given rules to the presented stimuli. Half of the verification probes were *true*, or reflected the answer that would be achieved if the correct rules were applied to the stimuli presented, and the other half of the probes were *false*, corresponding to the answer that would be achieved if an incorrect rule was applied to the stimuli presented. Sample stimuli for Spanish and English trials are listed in Table 2.

Handedness questionnaire

The Oldfield Handedness Inventory (Oldfield, 1971) was used to assess handedness of the participants. This survey includes 10 questions on which participants are asked to rate whether they do tasks using their left hand, right hand, or both hands equally. Handedness is then indexed as the relative proportion of right handed responses - left handed responses over the total number of right + left handed responses.

English proficiency measure

The English Grammatical Proficiency Test is a subtest of the "Examination for the Certificate of Proficiency in English" developed at the University of Michigan (English Language Institute, 2006). It has previously been used in bilingual investigations as a measure of English proficiency (e.g., van Hell and Tanner, 2012) as it is sensitive to subtleties in English grammatical proficiency. The subtest consists of 20 multiple choice questions and participants are given as much time as needed for completion.

Spanish proficiency measure

The Spanish Grammatical Proficiency test is a subtest of the standardized Spanish grammar proficiency test issued from the ministry of Spanish education for Diplomas in Spanish as a Foreign Language (el Ministerio de Educación, 1998). This multiple choice, paper and pencil test has also been previously used to assess Spanish proficiency in bilingual research (e.g., Montrul and Bowles, 2009). Participants were given as much time as they needed to complete the test.

Bilingual language experience questionnaire

A modified version of the Language Experience and Proficiency Questionnaire (Marian et al., 2007) was used as a self-report measure of bilingual language experience and proficiency. The test asks participants to self-rate language comprehension, production, and reading proficiency, and also asks explicit questions about background language experience. The modified version of this test has been used to characterize language experience in studies investigating individual differences in bilingual language experience (e.g., Yamasaki and Prat, 2014).

Procedure

Behavioral testing session

All participants completed behavioral testing before the fMRI session, with no more than two days between practice and neuroimaging sessions. The behavioral session included completion of the Edinburgh Handedness Inventory (Oldfield, 1971) and the language proficiency and experience measures above, in addition to two individual differences

Table 2Sample stimuli for spanish and english trials with sample experimental codes in parentheses.

Rule	English (#)		Spanish (*)		
	Stimulus	Response	Stimulus	Response	
Pronoun (1)	UNCLE	HE	TIÓ	EL	
Plural (2)	UNCLE	UNCLES	TIÓ	TIÓS	
Past (A)	WALK	WALKED	CAMINAR	CAMINARON	
Future (B)	WALK	WILL WALK	CAMINAR	CAMINARA	
Combination (1A)	UNCLE WALK	HE WALKED	TIÓ CAMINAR	EL CAMINARON	

measures collected on all participants in our lab, but not relevant for the study reported herein (Operation span: Unsworth et al., 2005; and Nelson-Denny Reading Test: Brown et al., 1993).

Following completion of these tasks, participants received systematic training on the RITL paradigm used for this experiment. The practice session was composed of a memory task in which participants memorized which language and which rules were associated with each symbol. Importantly for the current experiment, memory training for the RITL task was completed using instructions written in both Spanish and English. The memory task involved showing each of the code-rule pairs (e.g., "# - Spanish") three times in a random order, and participants were asked to type the corresponding code if a rule was given or to type a rule if a code is given. In order to complete the practice memory task, the participants had to reach a criterion of accurately identifying the same code at least two times consecutively. After completing the memory task, each participant completed 16 practice RITL trials. In the practice trials, participants were given explicit feedback on their performance including accuracy and response times to help ensure that they understood the task and could successfully perform it in the scanner. Altogether, the total behavioral session took 1.5 h.

fMRI data acquisition

Data were collected using a 3.0 T Philips Achieva scanner at the Integrative Brain Imaging Center operated by the University of Washington. The study was performed with a gradient echo planar pulse sequence with TR = 1000 ms, TE = 30 ms, a 60° flip angle and field of view = 240 mm. Seventeen oblique-axial slices were imaged, and each slice was 5-mm thick aligned to the anterior commissure-posterior commissure with a gap of 1 mm between slices. The acquisition matrix was 64×64 with an in-plane resolution of 3×3 mm voxels. For most participants, this did not constitute full coverage, and no data was collected from the most rostral and ventral parts of the temporal lobe, as well as from the regions surrounding the vertex. In the neuroimaging analysis procedures, any predefined region of interest that was not completely covered in all participants was excluded.

RITL Task

As is typical of RITL paradigms, presentation of all three phases were self-paced. Participants were instructed to press a button when they were finished encoding instructions (i.e., during the Prepare Target Language and Select Rule phases). During the Execute phase, participants were instructed to press a button after they had transformed the word(s) presented according to the rule(s) specified by the task. If no response was initiated within 8 s during Prepare Target Language, Select Rule, or Execute phases, the trial "timed out" and automatically advanced to the next phase (this occurred in 2% of the data). The duration of the *time out*

window was calculated based on pilot data as the value that contained all correct behavioral responding across the three phases in behavioral data collected out of the scanner.

Each trial ended with a verification probe. As is typical with RITL paradigms, the purpose of the verification probe is to ensure that participants are mentally generating the correct answer during the Execute phase. Thus, participants have only 2 s to respond YES for correct or NO for incorrect answers during the verification probe. To do so, they pressed a button with the hand corresponding to the position of the YES or NO labels on the screen. The position of the response labels was counterbalanced across participants. Accuracy to the verification probe is used to indicate which trials to use in subsequent analyses, however neural data is not analyzed during the verification phase.

To assess neural responses to the three critical task phases, each phase was separated from one another by delays with randomly varied durations between 1 and 12 s, according to an exponential distribution that optimizes parameter estimation (Dale, 1999). The purpose of these delays is to reduce the collinearity between phases, and allowed for better estimation of the brain activity corresponding to each phase. A schematic of a RITL trial presentation is depicted in Fig. 1.

fMRI data processing

fMRI preprocessing

The data were first preprocessed using SPM8 (Wellcome Trust Center for Neuroimaging, Cambridge, UK). All functional volumes were corrected for slice timing acquisition, realigned to the first image within each run, normalized to the Montreal Neurological Institute (MNI) template, resampled to 2 mm³ voxels, and smoothed using an 8 mm Gaussian kernel.

ROI analyses

To best integrate our results with those reported in the meta-analysis of Luk et al. (2012), which is reflective of the literature on bilingual language control at large, nine spherical regions of interest (ROIs) were used for ROI analyses. Centroids were converted from Talairach space to MNI space using Ginger ALE 2.3.3 (using the algorithm proposed by Brett et al., 2001). As the current experiment was critically interested in the ACC and BG, we added two additional regions that *did not reach significance* in the review paper, namely the left caudate nucleus and the anterior cingulate cortex (ACC). The size, reference from which the ROIs were drawn, original coordinates reported, MNI coordinates of the centroids, and corresponding Brodmann's areas (where applicable) of the nine ROIs used herein are listed in Table 3.

Summary statistics for the ROI analyses were generated by averaging across the parameter values (i.e., beta weights) of all voxels within the ROI. Summary statistics were calculated independently for each

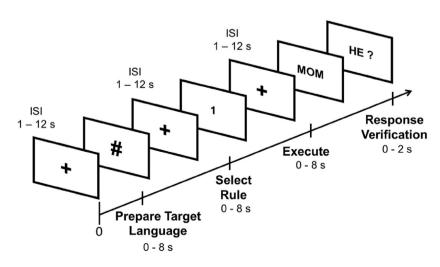


Fig. 1. Schematic of a sample trial from the Rapid Instructed Learning Task Paradigm.

Table 3Description of regions of interest (ROIs) used for neuroimaging analysis.

Region	Reference	Original Coordinates	Centroid MNI coordinates	BA	Radius (mm)
Left DLPFC	Luk et al. (2012)	-46, 18, 26	-44, 13, 29	46	8
	(Talairach Coordinates)				
Left Inferior Frontal	Luk et al. (2012)	-50, 18, 6	-48, 15, 11	44	8
	(Talairach Coordinates)				
Left Lateral Orbitofrontal	Luk et al. (2012)	-32, 20, -8	-31, 18, -2	47	8
	(Talairach Coordinates)				
Left Middle Temporal	Luk et al. (2012)	-50, -44, -6	-48, -42, -6	37	8
	(Talairach Coordinates)				
Pre-SMA	Luk et al. (2012)	2, 8, 58	1, 1, 57	6	10
	(Talairach Coordinates)				
Right Precentral	Luk et al. (2012)	44, -4, 30	40, -9, 32	6	8
	(Talairach Coordinates)				
Right Caudate	Luk et al. (2012)	16, 8, 12	14, 5, 16		6
	(Talairach Coordinates)				
Left Caudate	Left homologue of	-16, 8, 12	-14, 5, 16		6
	Luk et al. (2012) right caudate				
ACC	Abutalebi et al. (2011)	0, 6, 44	0, 32, 24		10
	(MNI Coordinates)				

combination of ROI, subject, and each of the three critical task phases (Prepare Target Language, Select Rule, Execute). The data were then analyzed separately for each ROI using one-way analyses of variance (ANOVAs), using the three task phases as the nominal levels of a single factor and subjects as the random factor. All effects were tested at a Bonferroni corrected significance level for 9 comparisons (p < .0056). Data from one participant was removed from the pre-SMA analysis as their slice prescription did not include the whole ROI.

Exploratory distribution of activation analyses

To examine the distribution of activation during the three critical task phases, statistical analyses were performed on individual and group data using the general linear model (GLM) implemented in SPM8 (Penny et al., 2007). Eight independent regressors were created corresponding to Preparation of Target Language, Rule Selection, Execution, and Verification phases in Spanish and English. Three types of analyses were conducted on the distribution of activation data. First, neural activity for the three critical task phases was estimated by collapsing across English and Spanish trials. Only trials in which participants responded correctly to the response verification probes were analyzed. Second, to address the three critical questions of interest, four statistical contrasts were computed between the three conditions (Prepare Target Language > Execute, Execute > Prepare Target Language, Prepare Target Language > Select Rule, and Select Rule > Prepare Target Language). Third, disjunction analyses were performed with the goal of determining patterns of activation unique to each of the four contrasts reported above. To do so, we started with the statistical contrasts reported above, and masked out any voxel that was active at a liberal threshold (p = .001 uncorrected) in the comparison or baseline condition. For instance, to determine which voxels were uniquely active in preparation, controlling for execution, any voxel active during Execution was removed from the contrast of Prepare Target Language > Execution. These analyses were modeled after those reported in Nee and Jonides (2013). For each analysis, group-level models were generated using the parameter estimates of first-level models as the summary statistics, and subjects as the random factor. To correct for multiple comparisons, all the results are reported after a family wise error (FWE) correction procedure at the voxel level, as implemented in SPM8, with corrected p < 0.05 and an extent threshold of 14 contiguous voxels to make sure that no cluster was found that was smaller than the smallest cluster that could be identified in native voxel space.

Results

Behavioral results

Accuracy rates to the response verification probes were high across

participants (M=88.5%, SEM=1.76%). Response times for correct trials were analyzed using a one-way repeated measures analysis of variance (ANOVA) with three within-participants task phases: Prepare Target Language (mean = 1547.57 ms, sem = 34.93), Select Rule (mean = 2726.83 ms sem = 47.69, and Execute (mean = 2953.33 ms, sem = 49.60). A significant main effect of task phase was revealed (F (2,66) = 57.570, p < 0.0001). Follow-up analyses showed that response times for Prepare Target Language were significantly shorter than for either Select Rule (f(22) = -12.684, p < 0.0001) or Execute (f(22) = -9.017, f = 0.0001) phases.

Another follow up analysis was conducted to compare performance across Spanish and English trial types. No significant differences were observed in response times across the three task phases (p > 0.4); however a comparison of task accuracies using Fisher's exact test revealed a trend towards better accuracy on English trials (p = .08).

Region of interest analyses

A significant main effect of task phase was observed in five of the nine ROIs: the anterior cingulate cortex (ACC), left dorsolateral prefrontal cortex (DLPFC), left lateral orbitofrontal cortex (BA 47), left inferior frontal gyrus (BA 44), and the pre-supplementary motor area (pre-SMA). Follow-up analyses showed that these phase-sensitive regions showed two different patterns of activation across the three tasks phases. Specifically, the ACC alone was significantly more active during the Prepare Target Language phase than during either Rule Selection or Execution phases, with the parameter estimates for the latter two being not significantly different than zero. In contrast, the three left frontal regions (left DLPFC, left orbitofrontal, left inferior frontal) and pre-SMA ROIs all showed significantly higher activation during the Execution phase than during the Prepare Target Language phase (with Rule Selection typically in between the two levels). Activation in the remaining four ROIs (bilateral caudate nuclei, left middle temporal gyrus, and right precentral gyrus) was not modulated by task phase, remaining constant across the task. F-statistics and follow up paired t-statistics are reported in Table 4. In summary, the ROI results suggest three unique patterns of activation across bilingual language control task phases: Preparatory Activation (greatest activation during preparation of target language), Execution Activation (activity that increases across task phases with highest activation during task execution), and Stable Activation (consistent activation across task phases). Patterns of activation in representative Preparation (ACC), Execution (DLPFC) and Stable (caudate) ROIs are depicted in Fig. 2.

Exploratory distribution of activation analyses

Voxel wise patterns of activation obtained from GLM estimates during

Table 4Statistics from One Way Repeated Measures ANOVA Analysis on Regions of Interest, and Follow up *t*-Tests.

Repeated Measures ANOVA Analysis	df	F	MSE	p
(A) Significant Main Effect of Phase				
Anterior cingulate cortex (ACC)	2	8.82	0.30	<.001
Left dorsolateral prefrontal cortex (DLPFC, BA 46)	2	25.50	0.41	<.001
Left lateral orbitofrontal cortex (BA 47)	2	15.32	0.12	<.001
Left inferior frontal gyrus (BA 44)	2	36.45	0.19	<.001
Presupplementary motor areas (pre-SMA)	2	6.10	0.34	0.005
(B) Nonsignificant Main Effect of Phase				
Left caudate nucleus	2	1.56	0.12	0.214
Right caudate nucleus	2	1.50	0.11	0.233
Left middle temporal gyrus (BA 37)	2	1.67	0.04	0.200
Right precentral gyrus (BA 6)	2	1.95	0.06	0.155
Follow-up Analysis (Paired Sample t-Test)	df	t	p	
ACC				
Prepare Target Language > Select Rule	22	3.77	0.001	
Prepare Target Language > Execute	22	3.32	0.003	
DLPFC				
Prepare Target Language > Select Rule	22	-3.14	0.005	
Prepare Target Language > Execute	22	-5.83	<.001	
Select Rule > Execute	22	-4.79	<.001	
Left lateral orbitofrontal cortex (BA 47)				
Prepare Target Language > Execute	22	-4.50	<.001	
Select Rule > Execute	22	-5.20	<.001	
Left inferior frontal gyrus (BA 44)				
PrepareTarget Language > Execute	22	-7.42	<.001	
Select Rule > Execute	22	-6.65	<.001	
pre-SMA				
pre-siviri				

Note. Follow up analysis (paired sample *t*-tests) was run only where applicable. Degrees of freedom in pre-SMA analyses reflect the fact that one less participant was included in this analysis due to lack of coverage of the ROI in acquisition.

the Prepare Target Language, Select Rule, and Execution phases, and statistical contrasts between these phases are described in the subsequent sections.

Prepare Target Language

GLM analysis revealed that preparing to use a target language resulted in the recruitment of a bilaterally distributed network including medial regions such as the ACC (BA 24 & 32), SMA, pre-SMA (BA6),

bilateral caudate nuclei, the left lateral prefrontal cortex (BA 44) and bilateral parietal regions (Table 5A). It is interesting to note that many of the regions typically associated with bilingual language control were activated during the preparatory phase of the task, in which no linguistic information was presented, and no task was being executed.

Select Rule

In contrast, the Select Rule phase recruited a more left-lateralized pattern of activation. Specifically, the activation was centered around the superior portion of the inferior frontal gyrus in the left hemisphere, extending into middle and superior frontal regions and into the precentral gyrus. Activation in bilateral BG and parietal regions was also observed (Table 5B).

Execute

As predicted, the inferior frontal gyrus (classic Broca's area or BA 44/45) was highly active during bilingual rule execution. This cluster of activation extended medially into insular cortex and BG regions. Bilateral parietal and occipital activation were also observed (Table 5C).

Preparation of target language versus execution

A statistical contrast between Prepare Target Language and Execution phases showed that preparing to use a language resulted in significantly greater activation in medial regions including anterior frontal (BA 10), anterior cingulate (BA 24), middle and posterior cingulate (BA 23), and precuneus regions. Additionally, greater activation was observed in the temporo-parietal junction in the left hemisphere (roughly Wernicke's area, BA 39) as well as in its right hemisphere homologue. Activation was also higher in the right middle temporal gyrus during the Prepare Target Language Phase (Table 6A). Disjunction analysis showed that the majority of these regions were also uniquely active during target language preparation (Table 6B).

In contrast, the primary cluster that was significantly more active during Execution than during the Prepare Target Language phase encompassed the left inferior and orbital frontal regions (BA 44, 45 & 47), including Broca's area. Bilateral occipital cortex was also more active during execution, likely due to the fact that in this phase participants were viewing more complex visual stimuli (words) as opposed to single symbols (Table 6C). Disjunction analysis showed that one region in the left inferior frontal gyrus and occipital regions were uniquely active in the Execution phase when Preparation was controlled for (Table 6D).

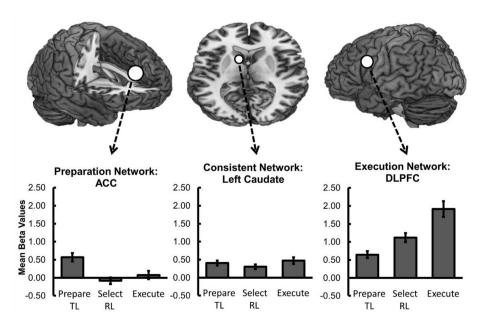


Fig. 2. Mean beta weights extracted across the three task phases from three regions that elicit different patterns across phases (ACC: Anterior Cingulate Cortex, DLPFC: Left Dorsolateral Prefrontal Cortex).

Table 5Centroids, cluster descriptions, and statistics for patterns of activation in three task phases (prepare target language, select rule, and execute).

Regions	Peak Cluste			MNI coordinates		
_	Brodmann's Area	Size	T Value	x	у	z
(A) Prepare Target La						
Bilateral anterior/ middle cingulate,	24	734	10.76	-10	6	52
Dorsolateral						
prefrontal, SMA						
Left precentral	4	277	7.79	-42	-6	24
eft postcentral	3	885	9.27	-54	-20	26
eft basal ganglia, insula, inferior frontal		1850	9.31	-20	2	18
eft superior/middle frontal		125	8.47	30	40	4
eft inferior parietal	40	618	9.98	-38	-56	42
eft superior temporal, parietal	39	158	7.01	-40	-48	12
eft hippocampus		50	6.88	-30	-30	4
eft inferior occipital	37 6	20 41	6.98 7.86	-50 44	−72 −6	-4 24
tight precentral tight cingulate	23	177	6.90	2	-0 -34	28
tight superior parietal	7	472	8.03	38	-66	52
tight superior/	10	56	6.55	22	56	16
frontopolar/						
dorsolateral frontal		001	0.05	10	_	
Right basal ganglia Right temporal	41	381 307	8.05 7.81	18 34	6 -30	14 0
tight inferior	37	51	7.64	34 44	-30 -70	-4
temporal	0,	01	7.01	• •	, 0	·
B) Select Rule						
ilateral SMA,	6	926	11.39	-6,	4	54
middle cingulate, DLPFC, superior/						
medial frontal,						
eft precentral	4	48	8.60	-32	2	60
ft thalamus, pre/		2868	9.99	-12	-20	8
post central,						
posterior cingulate,						
dorsolateral						
prefrontal, inferior						
frontal, insula,						
striatum						
eft insula	13	43	7.16	-46	6	2
eft caudate nucleus eft superior parietal	7	35 23	7.58 7.61	$-6 \\ -12$	24 -74	2 44
eft inferior parietal/	40	419	7.61 8.94	-12 -32	-74 -52	42
supramarginal	10	117	0.51	32	32	,2
ight precentral,		617	8.68	32	-10	28
caudate nucleus Light caudate		17	6.43	4	18	8
nucleus		15		1.4		
tight medial globus pallidus		17	7.74	14	-4	-2
Right thalamus		262	8.20	16	-20	10
Right middle	18	43	7.44	30	-94	2
occipital C) Execute						
eft inferior frontal,	44, 45	3492	12.77	-42	14	18
insula, superior/	,					
middle frontal,						
pre/postcentral,						
putamen, temporal		1606	0.71		_	
Bilateral supplementary	6	1606	9.74	-6	6	56
motor area,						
bilateral medial						
superior, bilateral						
dorsolateral						
frontal, right						
anterior/middle						
cingulate, superior,						
medial frontal						

Table 5 (continued)

Regions	Peak	Cluster	Peak	MNI co	MNI coordinates		
	Brodmann's Area	Size	T Value	x	у	z	
Left precentral	6	56	6.83	-30	0	58	
Left striatum		383	7.62	-20,	-2	2	
Left thalamus		184	7.50	-10	-18	4	
Left middle temporal	21	17	6.63	-58	-42	-6	
Left parietal, middle occipital	40	931	9.55	-30	-66	48	
Left middle occipital	18	136	8.00	-24	-96	2	
Right middle frontal		140	7.81	38	6	60	
Right insula	13	106	6.84	32	24	0	
Right striatum		275	7.82	12	2	-2	
Right parietal	7	194	6.77	32	-56	44	
Right calcarine	18	219	10.10	26	-96	2	

Note. MNI = Montreal Neurological Institute.

Selection of target language versus morpho-syntactic rule selection

A statistical contrast between the two types of task preparation indicated that activation was greater in the Prepare Target Language phase in the bilateral precuneus and middle temporal/supramarginal regions as well as in bilateral rostral and medial prefrontal regions, and bilateral temporo-parietal junctions (Table 7A and Fig. 4). Disjunction analyses showed that the majority of these regions were *uniquely* active during global target language selection, when morpho-syntactic rule selection was controlled for. There were no areas in which morphosyntactic rule selection resulted in greater activation than did global target language selection.

Discussion

The results from this experiment highlight the complexity of the information processing demands associated with bilingual language control. Specifically, they show that when top-down preparatory processes are investigated prior to linguistic task execution, and in the absence of bottom-up linguistic cues, distinct patterns of involvement emerge for the three core cognitive control regions (ACC, BG, and DLPFC), as well as from the broader network of regions previously implicated in bilingual language control. Below we organize our discussion of the current results around our three research questions.

How and when do general cognitive control regions participate in bilingual language control?

Our prediction for stable involvement of the BG across task phases was confirmed by the experimental results reported herein, which showed consistent activation of the bilateral striatum across task phases. These predictions are discussed in further detail in a review which proposes that the striatum is involved in "keeping track" of the target language a bilingual intends to communicate in, and uses this as a dynamic variable to route relevant, target-language-specific information to prefrontal cortex for subsequent processing (Stocco et al., 2014).

The idea that the striatum is involved in keeping track of which language a bilingual is using is consistent with previous research suggesting that language membership (e.g., English versus Spanish) is a feature of words in the bilingual brain that is accessible immediately, even before subsequent semantic category information (Hoverston et al., 2015). Given the priority of this information, it follows that the brain likely has a mechanism for determining which language a word form belongs to. Crinion's results from automatic within- and across-language semantic priming strongly suggest that the basal ganglia, and in particular the left caudate nucleus, is likely the center of such a language tracking mechanism (Crinion et al., 2006).

In the paradigm used for the current study, it is important to note that each phase of the task requires accessing *target language specific* information. During the Prepare Target Language phase, participants are first

Table 6Centroids, Cluster Descriptions, and Statistics for Contrasts and Disjunction Analyses between prepare target language and execute phases.

Regions	Peak	Cluster	Peak	MNI C	Coordina	tes
	Brodmann's Area	Size	T Value	x	у	z
(A) Prepare Target La	nguage (TL) >	Execute				
Bilateral superior and medial frontal, anterior cingulate	10	9.97	1512	18	54	20
Bilateral precuneus, posterior cingulate, middle cingulate, left cuneus		13.54	1192	-8	-60	36
Left superior temporal/ supramarginal, insula, post central	22	10.07	1103	-52	-12	4
Left angular	39	9.10	383	-50	-70	30
Left middle temporal	21	7.46	15	-64	-12	-14
Left fusiform, parahippocampal		6.60	16	-38	-42	-10
Median cingulum		6.85	116	0	-26	42
Right anterior cingulate cortex		6.53	26	2	36	18
Right precentral	43	7.22	397	56	-6	14
Right orbitofrontal	47	7.11	14	48	30	-8
Right middle orbitofrontal	10	6.97	19	30	58	-8
Right temporal, supramarginal, inferior parietal, middle occipita	40	9.70	1616	60	-58	16
(B) Prepare TL > Exec	ute (mask out.	Execute)				
Bilateral anterior cingulate		26	6.53	2	36	18
Left superior temporal, post central	22, 40	1103	10.07	-52	-12	4
Left angular	39	383	9.1	-50	-70	30
Left precuneus		1192	13.54	-8	-60	36
Left middle temporal	21	15	7.46	-64	-12	-14
Right superior frontal, medial frontal		1512	9.97	18	54	20
Right post central	43	397	7.22	56	-6	14
Right inferior frontal	45	14	7.11	48	30	-8
Right middle frontal	10	19	6.97	30	58	-8
Right temporal		1616	9.7	60	-58	16
(C) Execute > Prepare						
Left inferior frontal, precentral	44	8.03	650	-46	12	18
Left insula	13	6.73	51	-30	24	2
Left middle occipital	18	8.04	149	-20	-94	8
Right superior occipital	18	8.28	169	22	-96	16
(D) Execute > Prepare	e TL (mask out.	_				
Left inferior frontal		137	7.73	-56	24	20
Right cuneus		167	8.28	22	-96	16

 $\it Note.\ MNI = Montreal\ Neurological\ Institute.$

given the variable target language, and must store the current target language in memory. The subsequent Rule Selection phase requires that bilingual participants select the relevant rule for transforming a noun or verb based on the given target language. For instance, given the rule 1 (pronoun rule), bilinguals need to retrieve the appropriate rule for generating a feminine or masculine pronoun in either English (*she/he*) or Spanish (*ella/el*). Finally, during the Execution phase, participants are given a word in the target language, and must conjugate it according to language-specific rules previously provided. Although these phases likely involve different computations, each would require some kind of parameter setting based on the target language of a given trial.

Interestingly, although equivalent activation levels were observed in

Table 7Centroids, Cluster Descriptions, and Statistics for Contrasts and Disjunction Analyses between prepare target language and select rule.

Regions	Peak	Cluster	Peak T	MNI C	MNI Coordinates		
	Brodmann's Area	Size	Value	x	у	Z	
(A) Prepare Target	Language (TL) >	Select Rule	e (RL)				
Bilateral	7	6.96	33	-6	-60	38	
precuneus							
Left Inferior	47	6.66	28	-32	20	-18	
Frontal, Left							
Insula	20	6.45	07			00	
Left superior	39	6.45	37	-58	-58	28	
temporal/ Supramarginal							
Right inferior	47	7.48	100	48	32	-6	
orbitofrontal	47	7.40	100	40	32	-0	
Right superior,	46	7.27	218	18	54	20	
medial,	· -						
dorsolateral							
frontal							
Right middle	10	6.93	36	34	58	-8	
orbitofrontal							
Right superior		6.58	41	18	30	52	
frontal							
Right angular		6.54	69	60	-50	36	
Right superior		6.64	64	56	-52	18	
temporal							
(B) Prepare TL > So	elect RL (mask ou						
Left inferior frontal		28	6.66	-32	20	-18	
Left superior	39	37	6.45	-58	-58	28	
temporal		00		_		-	
Left precuneus	10.0	33	6.96	-6	-60	38	
Right superior frontal, medial	10, 9	218	7.27	18	54	20	
frontal							
Right superior		41	6.58	18	30	52	
frontal		71	0.50	10	30	32	
Right middle	10	36	6.93	34	58	-8	
frontal	-					-	
Right inferior		100	7.48	48	32	-6	
frontal							
Right		69	6.54	60	-50	36	
supramarginal							
Right superior	10	64	6.64	56	-52	18	
temporal							

Note. MNI = Montreal Neurological Institute.

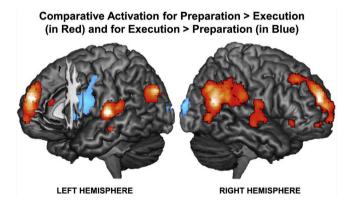


Fig. 3. Statistical contrasts for Prepare Target Language > Execute (in red) overlaid on the opposite contrast, Execute > Prepare Target Language (in blue).

bilateral striatal ROIs across phases, the different task phases did elicit spatially distinct regions within the basal ganglia circuit, especially in the right caudate nucleus. To illustrate, Fig. 5 depicts overlaid patterns of striatal activation for Preparation (in red), Rule Selection (in green), and Execution (in blue) with additive colors indicating overlap.

As is illustrated by the large white region in the left caudate, these

Comparative Activation for Preparation > Select Rule

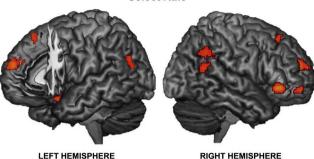


Fig. 4. Statistical contrasts for Prepare Target Language > Select Rule.

patterns of activation were highly overlapping in the left hemisphere; whereas, in the right caudate, the patterns of activation were more distinct across phases. These results may suggest that, consistent with the work of Crinion et al. (2006), and with the proposal made by Stocco et al. (2014), the left caudate keeps track of target language. The right caudate, on the other hand, has been suggested to be involved in inhibitory control or in overriding competing responses (e.g., Aron, 2011). Thus, it is possible that specific inhibitory control mechanisms are enacted at each task phase, based on the nature of information being blocked or gated to the prefrontal cortex. Consistent with this explanation, the right prefrontal region was also engaged in all task phases. We see the exploration of the role of the right caudate nucleus in bilingual language control as an important and interesting area for future investigation.

The results described herein also extend those initially reported by

Basal Ganglia Activation across Task Phases

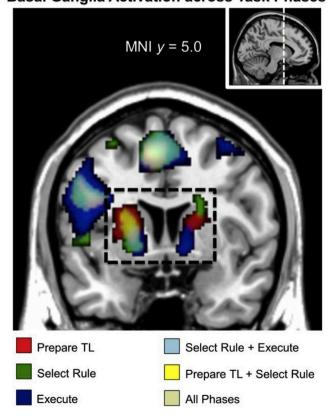


Fig. 5. Statistical activation maps depicting overlaid patterns of activation across the three task phases in the basal ganglia (left hemisphere located on left).

Hernandez et al. (2000) on the role of the DLPFC in bilingual language control. Consistent with our predictions and with previous research, we show that the DLPFC is activated during the sub-vocal production phase of our task. Our results extend those from previous research in two ways: (1) by showing that the DLPFC is active even under conditions in which task switching is not required, and (2) by showing that the DLPFC is also activated as the instructions for completing a task are sequentially presented, with the greatest activation occurring during task execution.

The DLPFC has been widely implicated in models of top-down cognitive control (e.g., Miller, 2000; Duncan, 2010; Braver, 2012), and the task used in this study was designed to isolate this form of control from the bottom-up influence of linguistic stimuli. It is possible that the increasing DLPFC activation across trials represents "goal maintenance," as the instructions for completing each trial are presented incrementally across the phases of the RITL task. It is also possible that the increase in activation across task phases may reflect an increase in working memory load, as participants must hold an increasing amount of information in mind in order to execute the appropriate rule (e.g., Cole and Schneider, 2007; Irlbacher et al., 2014). These findings are also consistent with research showing patterns of increasing activation in DLPFC with increased working memory as indexed by number of items to-be-remembered (e.g., Smith and Jonides, 1999).

It is important to note that the same increasing activation pattern was also observed in the left inferior frontal gyrus (BA44, BA47) and in the pre-SMA. The fact that the left inferior frontal gyrus was most active during morpho-syntactic rule execution is not particularly surprising, given its known role in both lexical selection (Thompson-Schill et al., 1997.; Vitello and Rodd, 2015) and morpho-syntactic rule related processes (Newman et al., 2003; Buchweitz and Prat, 2013). However, the pre-SMA has largely been proposed to be involved in conflict monitoring, perhaps proactively (Luk et al., 2012), and is often considered to work in concert with the ACC (e.g., Green and Abutalebi, 2013; Abutalebi and Green, 2016); this is surprisingly inconsistent with the pattern of results observed in the current experiment, which shows a rare dissociation of patterns of ACC and pre-SMA involvement. We see this as an interesting area for future research. Taken together, our results suggest that the DLPFC is part of a network of regions including the left lateral prefrontal cortex and pre-SMA that are most active during bilingual task execution.

It is unclear from our investigation, however, whether these prefrontal regions are engaged in the same neurocognitive processes, or implement different mechanisms that yield similar results in the current paradigm. In fact, recent bilingual language control models propose that left and right prefrontal regions may play different roles in language control (Abutalebi and Green, 2016). Although the current study did not have a right frontal ROI, both whole brain and ROI analyses suggested that left inferior and middle frontal regions were more active during execution than during preparation. In contrast, the whole brain analyses suggest that the right inferior frontal gyrus was more active during preparation than either during execution (Fig. 4) or rule selection (Fig. 5). These results are somewhat consistent with the idea put forth by Abutalebi and Green (2016) that the left inferior frontal regions are involved in language selection and the right inferior frontal regions are involved in response inhibition. Within this framework, our results suggest that selection and inhibition happen at different levels, with selection processes happening throughout the task on increasingly specific subsets of information (e.g., language, rule, item) and inhibition happening primarily at the global level (language). We see this as an interesting first step toward answering the question put forth in the same paper about whether "language control is exerted at a single level or at multiple levels." (Abutalebi and Green, 2016, p. 694).

The results on the role of the ACC in bilingual language control were contrary to our predictions. They suggested that the ACC was uniquely active during target language preparation (or global language selection). Specifically, our results extend and refine previous research on the role of the ACC in bilingual language control by showing that: (1) the ACC is active during target language preparation, even when it precedes task

execution, (2) the ACC was the only predefined ROI that was more active during target language preparation than during execution, and (3) ACC activation was not tied specifically to language switching.

A considerable amount of research has investigated the role of the ACC in domain-general cognitive control (e.g., Botvinick et al., 1999). Specifically, ACC activation is reliably observed in tasks involved in monitoring cognitive conflict such as overriding prepotent response and selecting a target among competing inputs (Badgaiyan and Posner, 1998; Carter et al., 1998; Carter et al., 1999; Ridderinkhof et al., 2004; Botvinick et al., 2004; Barber and Carter, 2004). In bilingual language control research specifically, ACC activity has been associated with monitoring language conflict (Abutalebi et al., 2007; Abutalebi et al., 2011). Such conflict has been typically operationalized in tasks such as picture naming paradigms in which the desired target language switches from trial to trial. It has been proposed that during such switching, conflict arises because two languages are competing for response selection and switching requires overriding the use of the current language (Van Heuven et al., 1998; 2008; De Groot et al., 2000).

Interestingly, our results show that ACC activation was not contingent on switching or overriding a previous response, as the preparation phases included both "switch" and "repeat" trials. Note that, however, our paradigm used a mixed design, with target language changing unpredictably from trial to trial. Thus, in these early and proficient bilinguals, language conflict was likely anticipated in our paradigm. In fact, our results suggest that the ACC may be engaged early to monitor the language in use at a global level under these language conflict conditions (Guo et al., 2011; Branzi et al., 2015). This interpretation is consistent with the results of Abutalebi et al. (2007), who showed that ACC activation was observed in bilingual language contexts, irrespective of whether the language of the trial is switched or repeated. With respect to preparatory processes more broadly, these results are also consistent with other findings in which ACC activation can be observed during cued preparation rather than during task execution (Luks et al., 2002; Fincham and Anderson, 2006; Sohn et al., 2007).

It is important to note that in our task, the classically defined ACC was *not* significantly involved in task execution (although more posterior portions of the mid-cingulate cortex were). The precise definition and location of the ACC ROI may explain why some previous bilingual language control paradigms implicate the ACC during task execution (Price et al., 1999; Abutalebi et al., 2007), while the current experiment does not. This also offers an alternate explanation of why the meta-analysis on bilingual language switching by Luk et al. (2012) did not find significant activation in the ACC across tasks. Taken together, these results highlight the importance of considering top-down preparatory processes in investigations of bilingual language control.

How do the neural networks involved in proactive control differ from those involved in bilingual language production?

Our ROI analysis revealed that five of the nine regions that have been repeatedly implicated in bilingual language control had significantly different responses during task preparation and task execution, highlighting the importance of considering these phases separately. Specifically, the three left frontal (DLPFC, inferior frontal, and orbital frontal) regions along with pre-SMA were all significantly more active during task execution than during preparation, whereas the ACC was significantly more active during task preparation. The remaining four regions including the bilateral BG, left middle temporal, and right precentral ROIs, were equally active during preparation and execution.

These results, combined with those from the whole-brain analyses, partially overlap with those reported by Reverberi et al. (2015). First and foremost, both experiments implicate the precuneus and the left posterior temporal regions in Target Language Preparation (see Fig. 3). Reverberi and colleagues propose that the precuneus activation is part of a broader "fronto-parietal control network responsible for directing selective attention" (Reverberi et al., 2015, p.8). It is notable that our preparation

activation did include a broader fronto-parietal network, whereas theirs did not (see subsequent discussion of design differences). Interestingly, the precuneus has also been associated with thoughts of self (Northoff and Bermpohl, 2004; Cavanna and Trimble, 2006), internalized focus of attention (Mason et al., 2007), or the default mode network (Fox et al., 2005). Thus, it is possible that when bilingual individuals globally select or prepare to use a target language, some broader activation of different senses of "self" occurs. This is particularly interesting when considered in light of social-cognitive research on bicultural individuals, suggesting that different patterns of thinking and behaving can be primed by culture-specific scenarios (e.g., Benet-Martínez et al., 2002).

One key difference between our results and those previously reported is that we found the medial prefrontal region (BA10) to be more involved in task preparation than task execution, whereas Reverberi et al. (2015) found this region to be implicated in task execution. This is not particularly troubling, since the contrasts reported herein differ in important ways from those reported by Reverberi. Specifically, Reverberi et al. (2015) contrasted activation in trials in which target language switched, from those in which target language repeated, looking separately at preparation and execution phases. In contrast, we looked at all trials in a mixed language design, and contrasted the preparation and execution phases directly. Therefore, it is possible that BA 10 is always active during preparation (especially in a mixed design as both experiments were), and is only active when conflict is high during execution of switch trials. This pattern would produce the results obtained in both experiments. Finally, it is important to note that Reverberi et al. (2015) found that the ACC and BG were particularly active during execution of trials in a non-dominant L2; however, our participants were early bilinguals with relatively balanced proficiency in both languages, and thus, these contrasts have little relevance for the current study.

How do the neural networks involved in global language selection differ from those involved in morpho-syntactic rule selection?

In the current experiment, we investigated whether the type of control necessary for selecting a target language to speak in, and subsequently selecting the appropriate morpho-syntactic rule within that language differed. The difference between such global target selection and more local selection of rules and word forms within that language is central to the Adaptive Control Hypothesis described by Green and Abuatalebi (2013). Both types of preparation resulted in distributed activation in bilateral fronto-parietal networks, medial frontal regions, and the BG (see Table 6). Target language preparation, however, recruited more activation overall, with activation in the rostral prefrontal cortex, the ACC, and bilateral temporo-parietal regions being uniquely active. In contrast, there were no regions that were more active, or uniquely active during morpho-syntactic rule selection.

This pattern of results is consistent with the proposal made by Buchweitz and Prat (2013), that target language may be represented hierarchically in bilingual morpho-syntactic representations. However, as discussed in the previous sections, the fronto-parietal and medial networks observed during target language preparation are also consistent with a more general, top-down attention biasing network. Because target language information was always given at the beginning of a trial, it is possible that the greater activation in these regions simply reflects a strong response to the first cue about the upcoming trial. Future work investigating the processes involved in global language selection versus more specific lexical or morpho-syntactic processes may also want to account for order effects to control for this.

Conclusions and caveats

Up until this point, we have focused on the response profiles of individual regions including the ACC, BG, and DLPFC across the various phases of our bilingual language control task. A mechanistic explanation of how these regions accomplish bilingual language control, however, R. Seo et al. NeuroImage 174 (2018) 44-56

requires a more complete understanding of how and when these regions interact and influence one another. In a recent dynamic causal modeling analysis, Becker and colleagues investigated such interactions by comparing models with different patterns of effective connectivity between the ACC, BG, and DLPFC in monolingual and bilingual individuals as they executed a non-linguistic RITL task (Becker et al., 2016). They found that the model in which the ACC exerted increased influence over both DLPFC and the BG during the condition that required the most control, novel task execution, best fit the data of both monolinguals and bilinguals. Additionally, they found differences in the strength and direction of these influences between monolinguals and bilinguals. The authors concluded that these differences are shaped by the increased demands for cognitive control in bilingual individuals. The fact that ACC activity was observed at the beginning of each trial, and preceded increased activation in the DLPFC may suggest a similar pattern of influence between these regions in the current experiment. To test this directly, future experiments should measure the effective connectivity between the language control regions discussed herein.

The interconnectivity of these regions can also be inferred from their co-reliance on dopamine pathways. For example, a recent experiment by Vaughn et al. (2016) found that variation in *DRD2*, a gene that relates to expression of dopamine receptors in the BG, predicts differences in neural activity in the inferior frontal gyrus and anterior cingulate cortex during linguistic and non-linguistic cognitive control tasks (Vaughn et al., 2016). In fact, Stocco and colleagues have proposed that bilinguals experience places extra demands in the dopamine gating system for target language selection and use, and that these demands may shape cognitive control more broadly (Stocco et al., 2010; Stocco and Prat, 2014). One interesting link between these two papers was recently reported by Hernandez and colleagues (Hernandez et al., 2015), who found that in the college population tested, different proportions of the *DRD2/ANKK1* polymorphism were observed between the bilinguals and monolinguals.

An additional limitation of this experiment is that to explore topdown language control mechanisms, we used symbolic cues to inform participants which language they would be using and which morphosyntactic manipulation they would be performing. In doing so, we have arguably created a task that is more like a canonical cognitive control task than it is like a natural language task. In fact, the task is quite artificial, with no linguistic material being presented until the last phase of the task. Although this argument can be made of many controlled laboratory studies, subsequent research is needed to determine the extent to which the neural networks outlined herein are active in more naturalistic settings, such as when a bilingual views the face of an individual known to speak one language or another. In fact, one recent experiment on bilingual language switching showed that conditions in which natural contexts (faces) preceded a switching task, less ACC and PFC activity were observed than in conditions where more arbitrary cues (colored squares) preceded the task (Blanco-Elorrieta and Pylkkanen, 2017).

Despite these limitations, the results reported herein extend the body of research implicating general cognitive control regions in bilingual language control by showing that three core regions, the DLPFC, the BG, and the ACC, exhibit different patterns of activation across a bilingual morpho-syntactic rule production task. When viewed in light of existing research on both bilingual language control and cognitive control more broadly, we propose that the ACC may be involved in detecting language conflict at the earliest possible point, and using that information to trigger the fronto-striatal signal biasing system discussed by Stocco et al. (2014). The BG keep track of the target language and use this information to weigh competing signals, which converge on a structured network of rules for responding in the DLPFC.

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Supplementary material

The experimental stimuli and data (including individual de-identified datasets, individual statistical analysis, group-level results, and the MATLAB and shell scripts to reproduce the analyses) are freely available on the Harvard Dataverse: https://doi.org/10.7910/DVN/W6WJVN.

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References

- Abutalebi, J., Green, D., 2007. Bilingual language production: the neurocognition of language representation and control. J. Neurolinguistics 20 (3), 242–275.
- Abutalebi, J., Green, D.W., 2016. Neuroimaging of language control in bilinguals: neural adaptation and reserve. Biling. Lang. Cognit. 19 (4), 689–698.
- Abutalebi, J., Miozzo, A., Cappa, S.F., 2000. Do subcortical structures control 'language selection' in polyglots? Evidence from pathological language mixing. Neurocase 6 (1), 51–56.
- Abutalebi, J., Annoni, J.M., Zimine, I., Pegna, A.J., Seghier, M.L., Lee-Jahnke, H., Khateb, A., 2007. Language control and lexical competition in bilinguals: an eventrelated fMRI study. Cerebr. Cortex 18 (7), 1496–1505.
- Abutalebi, J., Della Rosa, P.A., Green, D.W., Hernandez, M., Scifo, P., Keim, R., Costa, A., 2011. Bilingualism tunes the anterior cingulate cortex for conflict monitoring. Cerebr. Cortex 22 (9), 2076–2086.
- Aron, A.R., 2011. From reactive to proactive and selective control: developing a richer model for stopping inappropriate responses. Biol. Psychiatr. 69 (12), e55–e68.
- Badgaiyan, R.D., Posner, M.I., 1998. Mapping the cingulate cortex in response selection and monitoring. Neuroimage 7 (3), 255–260.
- Badre, D., 2008. Cognitive control, hierarchy, and the rostro-caudal organization of the frontal lobes. Trends Cognit. Sci. 12 (5), 193–200.
- Barber, A.D., Carter, C.S., 2004. Cognitive control involved in overcoming prepotent response tendencies and switching between tasks. Cerebr. Cortex 15 (7), 899–912.
- Becker, T.M., Prat, C.S., Stocco, A., 2016. A network-level analysis of cognitive flexibility reveals a differential influence of the anterior cingulate cortex in bilinguals versus monolinguals. Neuropsychologia 85, 62–73.
- Benet-Martínez, V., Leu, J., Lee, F., Morris, M.W., 2002. Negotiating biculturalism: cultural frame switching in biculturals with oppositional versus compatible cultural identities. J. Cross Cult. Psychol. 33 (5), 492–516.
- Blanco-Elorrieta, E., Pylkkänen, L., 2017. Bilingual language switching in the laboratory versus in the wild: the spatiotemporal dynamics of adaptive language control. J. Neurosci. 37 (37), 9022–9036.
- Botvinick, M., Nystrom, L.E., Fissell, K., Carter, C.S., Cohen, J.D., 1999. Conflict monitoring versus selection-for-action in anterior cingulate cortex. Nature 402 (6758), 179–181.
- Botvinick, M.M., Cohen, J.D., Carter, C.S., 2004. Conflict monitoring and anterior cingulate cortex: an update. Trends Cognit. Sci. 8 (12), 539–546.
- Branzi, F.M., Della Rosa, P.A., Canini, M., Costa, A., Abutalebi, J., 2015. Language control in bilinguals: monitoring and response selection. Cerebr. Cortex 26 (6), 2367–2380.
- Braver, T.S., 2012. The variable nature of cognitive control: a dual mechanisms framework. Trends Cognit. Sci. 16 (2), 106–113.
- Braver, T.S., Gray, J.R., Burgess, G.C., 2007. Explaining the many varieties of working memory variation: dual mechanisms of cognitive control. Var. Work. Mem. 76–106.Brett, M., Christoff, K., Cusack, R., Lancaster, J., 2001. Using the Talairach atlas with the MNI template. Neuroimage 13 (6), 85–85.
- Brown, J.I., Fishco, V.V., Hanna, G., 1993. Nelson-denny Reading Test: Manual for Scoring and Interpretation Forms G & H. Riverside Publishing, Rolling Meadows, IL.
- Buchweitz, A., Prat, C., 2013. The bilingual brain: flexibility and control in the human cortex. Phys. Life Rev. 10 (4), 428–443.Carter, C.S., Braver, T.S., Barch, D.M., Botvinick, M.M., Noll, D., Cohen, J.D., 1998.
- Anterior cingulate cortex, error detection, and the online monitoring of performance. Science 280 (5364), 747–749.
- Carter, C.S., Botvinick, M.M., Cohen, J.D., 1999. The contribution of the anterior cingulate cortex to executive processes in cognition. Rev. Neurosci. 10 (1), 49–58.
- Cavanna, A.E., Trimble, M.R., 2006. The precuneus: a review of its functional anatomy and behavioural correlates. Brain 129 (3), 564–583.
- Cole, M.W., Schneider, W., 2007. The cognitive control network: integrated cortical regions with dissociable functions. Neuroimage 37 (1), 343–360.
- Cole, M.W., Bagic, A., Kass, R., Schneider, W., 2010. Prefrontal dynamics underlying rapid instructed task learning reverse with practice. J. Neurosci. 30 (42), 14245–14254.

R. Seo et al. NeuroImage 174 (2018) 44-56

- Cole, M.W., Laurent, P., Stocco, A., 2013. Rapid instructed task learning: a new window into the human brain's unique capacity for flexible cognitive control. Cognit. Affect Behav. Neurosci. 13 (1), 1–22.
- Costa, A., Miozzo, M., Caramazza, A., 1999. Lexical selection in bilinguals: do words in the bilingual's two lexicons compete for selection? J. Mem. Lang. 41 (3), 365–397.
- Crinion, J., Turner, R., Grogan, A., Hanakawa, T., Noppeney, U., Devlin, J.T., Usui, K., 2006. Language control in the bilingual brain. Science 312 (5779), 1537–1540.
- Dale, A.M., 1999. Optimal experimental design for event-related fMRI. Hum. Brain Mapp. 8 (2–3), 109–114.
- Duncan, J., 2010. The multiple-demand (MD) system of the primate brain: mental programs for intelligent behaviour. Trends Cognit. Sci. 14 (4), 172–179.
- el Ministerio de Educación, 1998. Diplomas de español (DELE). University of Salamanca and Instituo Cervantes.
- English Language Institute, 2006. Examination for the certificate of proficiency in English: information bulletin. English Language Institute, University of Michigan, Ann Arbor
- Fabbro, F., 2001. The bilingual brain: cerebral representation of languages. Brain Lang. 79 (2), 211–222.
- Fincham, J.M., Anderson, J.R., 2006. Distinct roles of the anterior cingulate and prefrontal cortex in the acquisition and performance of a cognitive skill. Proc. Natl. Acad. Sci. Unit. States Am. 103 (34), 12941–12946.
- Fox, M.D., Snyder, A.Z., Vincent, J.L., Corbetta, M., Van Essen, D.G., Raichle, M.E., 2005. The human brain is intrinsically organized into dynamic, anticorrelated functional networks. Proc. Natl. Acad. Sci. U.S.A. 102 (27), 9673–9678.
- Green, D.W., Abutalebi, J., 2013. Language control in bilinguals: the adaptive control hypothesis. J. Cognit. Psychol. 25 (5), 515–530.
- De Groot, A.M., Delmaar, P., Lupker, S.J., 2000. The processing of interlexical homographs in translation recognition and lexical decision: support for non-selective access to bilingual memory. Q. J. Exp. Psychol.: Section A 53 (2), 397–428.
- Guo, T., Liu, H., Misra, M., Kroll, J.F., 2011. Local and global inhibition in bilingual word production: fMRI evidence from Chinese–English bilinguals. Neuroimage 56 (4), 2300–2309.
- Hatzidaki, A., Branigan, H.P., Pickering, M.J., 2011. Co-activation of syntax in bilingual language production. Cognit. Psychol. 62 (2), 123–150.
- Van Hell, J.G., Tanner, D., 2012. Second language proficiency and cross-language lexical activation. Lang. Learn. 62 (s2), 148–171.
- Hernandez, A.E., 2009. Language switching in the bilingual brain: what's next? Brain Lang. 109 (2), 133–140.
- Hernandez, A.E., Martinez, A., Kohnert, K., 2000. In search of the language switch: an fMRI study of picture naming in Spanish–English bilinguals. Brain Lang. 73 (3),
- 421–431.
 Hernandez, A.E., Dapretto, M., Mazziotta, J., Bookheimer, S., 2001. Language switching and language representation in Spanish–English bilinguals: an fMRI study. Neuroimage 14 (2), 510–520.
- Hernandez, A.E., Greene, M.R., Vaughn, K.A., Francis, D.J., Grigorenko, E.L., 2015.Beyond the bilingual advantage: the potential role of genes and environment on the development of cognitive control. J. Neurolinguistics 35, 109–119.
- Van Heuven, W.J., Dijkstra, T., Grainger, J., 1998. Orthographic neighborhood effects in bilingual word recognition. J. Mem. Lang. 39 (3), 458–483.
- Van Heuven, W.J., Schriefers, H., Dijkstra, T., Hagoort, P., 2008. Language conflict in the bilingual brain. Cerebr. Cortex 18 (11), 2706–2716.
- Hoversten, L.J., Brothers, T., Swaab, T.Y., Traxler, M.J., 2015. Language membership identification precedes semantic access: suppression during bilingual word recognition. J. Cognit. Neurosci. 27 (11), 2108–2116.
- Irlbacher, K., Kraft, A., Kehrer, S., Brandt, S.A., 2014. Mechanisms and neuronal networks involved in reactive and proactive cognitive control of interference in working memory. Neurosci. Biobehav. Rev. 46, 58–70.
- Kerns, J.G., Cohen, J.D., MacDonald, A.W., Cho, R.Y., Stenger, V.A., Carter, C.S., 2004. Anterior cingulate conflict monitoring and adjustments in control. Science 303 (5660), 1023–1026.
- Koechlin, E., Ody, C., Kouneiher, F., 2003. The architecture of cognitive control in the human prefrontal cortex. Science 302 (5648), 1181–1185.
- Lehtonen, M.H., Laine, M., Niemi, J., Thomsen, T., Vorobyev, V.A., Hugdahl, K., 2005. Brain correlates of sentence translation in Finnish–Norwegian bilinguals. Neuroreport 16 (6), 607–610.
- Luk, G., Green, D.W., Abutalebi, J., Grady, C., 2012. Cognitive control for language switching in bilinguals: A quantitative meta-analysis of functional neuroimaging studies. Lang. Cognit. Process. 27 (10), 1479–1488.
- Luks, T.L., Simpson, G.V., Feiwell, R.J., Miller, W.L., 2002. Evidence for anterior Cingulate cortex involvement in monitoring preparatory attentional set. Neuroimage 17 (2), 792–802.
- Mansouri, F.A., Tanaka, K., Buckley, M.J., 2009. Conflict-induced behavioural adjustment: a clue to the executive functions of the prefrontal cortex. Nat. Rev. Neurosci. 10 (2), 141–152.
- Marian, V., Blumenfeld, H.K., Kaushanskaya, M., 2007. The language experience and proficiency Questionnaire (LEAP-Q): assessing language profiles in bilinguals and multilinguals. J. Speech Lang. Hear. Res. 50 (4), 940–967.
- Mason, M.F., Norton, M.I., Van Horn, J.D., Wegner, D.M., Grafton, S.T., Macrae, C.N., 2007. Response to comment on Wandering Minds: the default network and stimulusindependent thought. Science 317 (5834), 43.

Miller, E.K., 2000. The prefontral cortex and cognitive control. Nat. Rev. Neurosci. 1 (1), 59–65

- Miller, E.K., Cohen, J.D., 2001. An integrative theory of prefrontal cortex function. Annu. Rev. Neurosci. 24 (1), 167–202.
- Montrul, S., Bowles, M., 2009. Back to basics: incomplete knowledge of differential object marking in Spanish heritage speakers. Biling. Lang. Cognit. 12 (3), 363–383.
- Nee, D.E., Jonides, J., 2013. Neural evidence for a 3-state model of visual short-term memory. Neuroimage 74, 1–11.
- Newman, S.D., Just, M.A., Keller, T.A., Roth, J., Carpenter, P.A., 2003. Differential effects of syntactic and semantic processing on the subregions of Broca's area. Cognit. Brain Res. 16 (2), 297–307.
- Northoff, G., Bermpohl, F., 2004. Cortical midline structures and the self. Trends Cognit. Sci. 8 (3), 102–107.
- Oldfield, R.C., 1971. The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9 (1), 97–113.
- Pasupathy, A., Miller, E.K., 2005. Different time courses of learning-related activity in the prefrontal cortex and striatum. Nature 433 (7028), 873–876.
- Penny, W., Friston, K., Ashburner, J., Kiebel, S., Nichols, T., 2007. Statistical Parametric Mapping: the Analysis of Functional Brain Images.
- Pickering, M.J., Ferreira, V.S., 2008. Structural priming: a critical review. Psychol. Bull. 134 (3), 427.
- Price, C.J., Green, D.W., Von Studnitz, R., 1999. A functional imaging study of translation and language switching. Brain 122 (12), 2221–2235.
- Reverberi, C., Kuhlen, A., Abutalebi, J., Greulich, R.S., Costa, A., Seyed-Allaei, S., Haynes, J.D., 2015. Language control in bilinguals: intention to speak vs. execution of speech. Brain Lang. 144, 1–9.
- Ridderinkhof, K.R., Ullsperger, M., Crone, E.A., Nieuwenhuis, S., 2004. The role of the medial frontal cortex in cognitive control. Science 306 (5695), 443–447.
- Robles, S.G., Gatignol, P., Capelle, L., Mitchell, M.C., Duffau, H., 2005. The role of dominant striatum in language: a study using intraoperative electrical stimulations. J. Neurol. Neurosurg. Psychiatr. 76 (7), 940–946.
- Ruge, H., Jamadar, S., Zimmermann, U., Karayanidis, F., 2013. The many faces of preparatory control in task switching: reviewing a decade of fMRI research. Hum. Brain Mapp. 34 (1), 12–35.
- Smith, E.E., Jonides, J., 1999. Storage and executive processes in the frontal lobes. Science 283 (5408), 1657–1661.
- Sohn, M.H., Carlson, R.A., 2000. Effects of repetition and foreknowledge in task-set reconfiguration. J. Exp. Psychol. Learn. Mem. Cognit. 26 (6), 1445.
- Sohn, M.H., Albert, M.V., Jung, K., Carter, C.S., Anderson, J.R., 2007. Anticipation of conflict monitoring in the anterior cingulate cortex and the prefrontal cortex. Proc. Natl. Acad. Sci. Unit. States Am. 104 (25), 10330–10334.
- Stocco, A., Prat, C.S., 2014. Bilingualism trains specific brain circuits involved in flexible rule selection and application. Brain Lang. 137, 50–61.
- Stocco, A., Lebiere, C., Anderson, J.R., 2010. Conditional routing of information to the cortex: a model of the basal ganglia's role in cognitive coordination. Psychol. Rev. 117 (2), 541.
- Stocco, A., Lebiere, C., O'Reilly, R.C., Anderson, J.R., 2012. Distinct contributions of the caudate nucleus, rostral prefrontal cortex, and parietal cortex to the execution of instructed tasks. Cognit. Affect Behav. Neurosci. 12 (4), 611–628.
- Stocco, A., Yamasaki, B., Natalenko, R., Prat, C.S., 2014. Bilingual brain training: a neurobiological framework of how bilingual experience improves executive function. Int. J. BiLing, 18 (1), 67–92.
- Thompson-Schill, S.L., D'Esposito, M., Aguirre, G.K., Farah, M.J., 1997. Role of left inferior prefrontal cortex in retrieval of semantic knowledge: a reevaluation. Proc. Natl. Acad. Sci. Unit. States Am. 94 (26), 14792–14797.
- Unsworth, N., Heitz, R.P., Schrock, J.C., Engle, R.W., 2005. An automated version of the operation span task. Behav. Res. Meth. 37 (3), 498–505.
- Vaughn, K.A., Nunez, A.I.R., Greene, M.R., Munson, B.A., Grigorenko, E.L., Hernandez, A.E., 2016. Individual differences in the bilingual brain: the role of language background and DRD2 genotype in verbal and non-verbal cognitive control. J. Neurolinguistics 40, 112–127.
- Vitello, S., Rodd, J.M., 2015. Resolving semantic ambiguities in sentences: cognitive processes and brain mechanisms. Lang. Ling. Comp. 9 (10), 391–405.
- Wallis, J.D., Anderson, K.C., Miller, E.K., 2001. Single neurons in prefrontal cortex encode abstract rules. Nature 411 (6840), 953–956.
- Wang, Y., Kuhl, P.K., Chen, C., Dong, Q., 2009. Sustained and transient language control in the bilingual brain. Neuroimage 47 (1), 414–422.
- Wiktionary, 2017a. Spanish Frequency List; [cited 2017 Sept 11]. Available from: https://en.wiktionary.org/wiki/User:Matthias_Buchmeier#Spanish_frequency_list.
- Wiktionary, 2017b. English Frequency List; [cited 2017 Sept 11]. Available from: https://en.wiktionary.org/wiki/Wiktionary:Frequency_lists.
- Woumans, E., Martin, C.D., Vanden Bulcke, C., Van Assche, E., Costa, A., Hartsuiker, R.J., Duyck, W., 2015. Can faces prime a language? Psychol. Sci. 26 (9), 1343–1352.
- Yamasaki, B.L., Prat, C.S., 2014. The importance of managing interference for second language reading ability: an individual differences investigation. Discourse Process 51 (5–6), 445–467.
- Zhang, S., Morris, M.W., Cheng, C.Y., Yap, A.J., 2013. Heritage-culture images disrupt immigrants' second-language processing through triggering first-language interference. Proc. Natl. Acad. Sci. Unit. States Am. 110 (28), 11272–11277.