Functional dynamics of dorsal and ventral reading networks in bilinguals

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Abstract

In today's world bilingualism is increasingly common. However, it is still unclear how left-lateralized dorsal and ventral reading networks are tuned to reading in proficient second language learners. Here, we investigated differences in functional regional activation and connectivity as a function of L1 and L2 reading, L2 orthographic depth and task demands. Thirty-seven late bilinguals with the same L1 and either an opaque or transparent L2 performed perceptual and semantic reading tasks in L1 and L2 during fMRI scanning. Results revealed stronger regional recruitment for L2 versus L1 reading and stronger connectivity within the dorsal stream during L1 versus L2 reading. Differences in orthographic depth were associated with a segregated profile of left ventral occipitotemporal (vOT) coactivation with dorsal regions for the transparent L2 group and with ventral regions for the opaque L2 group. Finally, semantic versus perceptual demands modulated left vOT engagement, supporting the interactive account of the contribution of vOT to reading, and were associated with stronger coactivation within the ventral network. Our findings support a division of labor between ventral and dorsal reading networks, elucidating the critical role of the language used to read, L2 orthographic depth and task demands on the functional dynamics of bilingual reading.

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Over half of the world's population is already bilingual (Grosjean, 2010) and substantial efforts have been made to implement bilingual educational programs in predominantly monolingual societies. Bilingualism is, thus, both a reality and a desired goal in today's world. Although we know that learning to read entails a substantial reorganization of the brain (Carreiras et al. 2009), there are still many unanswered questions concerning bilingual reading: What regional and connectivity patterns among left perisylvian regions support reading in the first (L1) and in the second language (L2)? To what extent does reading rely on different neural dynamics as a function of the orthographic depth of a language? Do orthographic depth and reading demands modulate the recruitment of ventral and dorsal reading networks in bilinguals?

Neuroimaging research has shown a differential involvement of dorsal and ventral routes in reading processes in studies with monolingual samples (Pugh et al. 2001; Schlaggar and McCandliss 2007). Whereas the dorsal pathway, encompassing parietal lobe, superior temporal gyrus (STG) and inferior frontal gyrus (IFG) *pars opercularis*, is thought to subserve phonological processing, the ventral pathway, including vOT and anterior IFG regions (i.e., *pars triangularis and pars obitalis*), supports mapping of orthographic-lexical stimuli onto semantic representations (Sandak et al. 2004). These findings have also been bolstered by studies looking at white-matter pathways (Saur et al. 2008; Rolheiser et al. 2011; Friederici, 2012). Although results in studies with monolingual samples show a differential engagement of dorsal versus ventral reading regions, there is limited evidence as to what extent similar functional involvement of these networks is present in bilingual reading, and which aspects of reading (e.g., direct phonology *versus* assembled phonology) modulate their recruitment.

Evidence from the few available neuroimaging studies investigating bilingual reading has shown differences in regional activation profiles based on the L2 age-of-acquisition (AoA;

Perani et al. 2003; Wartenburger et al. 2003), language proficiency (Meschyan and Hernández, 2006), and language orthography (Meschyan and Hernández, 2006; Das et al. 2011; Jamal et al. 2012). Overall, results from these studies revealed an extensive overlap in the language regions engaged for L1 and L2 reading in early, but not in late bilinguals (Wartenburger et al. 2003). In late bilinguals, differences for L2 reading have been attributed largely to reduced reading proficiency in the L2 (Meschyan and Hernandez, 2006), with higher proficiency levels associated with higher overlap in L1 and L2 reading (Perani and Abutalebi, 2005). Nevertheless, there is also evidence for differences in the neural correlates associated with L2 reading in high-proficient late bilinguals, which have been attributed to the greater effort required when reading in the L2 (Wartenburger et al. 2003). Regarding language orthography, several studies have suggested that orthographic depth may modulate the engagement of regions along the dorsal and ventral networks. Reading in transparent orthographies with a strong letter-to-sound correspondence (e.g., Spanish or Italian) may rely more on phonological processes supported by dorsal regions, while reading in opaque orthographies (e.g., English) may rely more on lexico-semantic processes supported by the ventral pathway (Paulesu et al. 2000; Meschyan and Hernández, 2006; Das et al. 2011; Rueckl et al. 2015).

Here, we sought to investigate the involvement of regions along the dorsal and ventral networks in bilingual reading as a function of the native versus non-native language used to read (i.e., L1, L2) and L2 orthographic depth (i.e., opaque, transparent). To this end, we controlled for AoA and language proficiency, selecting two groups of late sequential reading bilinguals composed of native Spanish-speakers who have an L2 with a orthography that is either opaque (English; Spanish-English group) or transparent (Basque; Spanish-Basque group). Both groups acquired L1 reading first and then L2 reading after 6 years of age and have similar high

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proficiency levels in their L1 and L2. An additional main motivation of the present study was to examine to what extent the involvement of the dorsal and ventral networks in bilingual reading and the recruitment of the left vOT depends on the demands posed by the reading task. Most reading studies conducted with monolingual and bilingual populations have used either low-level (i.e., passive reading) or high-level (i.e., reading for meaning) reading tasks and, to date, no studies have examined within the same bilingual sample the influence of reading demands. Placing perceptual or semantic task demands on reading processes can modulate the neural computations carried out by dorsal and ventral reading networks, and especially by the left vOT within the ventral stream.

The left vOT plays a crucial role in reading and has been proposed as a critical site for orthographic processing during visual word recognition. However, its functional role is still the subject of important debate. Some theoretical accounts highlight its involvement in bottom-up prelexical computation processes of visual word forms (Dehaene and Cohen 2011), while others emphasize its implication in integrating visuospatial features abstracted from sensory inputs with higher-level associations, *via* bottom-up and top-down connections (Price and Devlin 2011). Interestingly, studies supporting a prelexical computational role of the vOT have mainly used low-level reading tasks (e.g., passive silent reading; Cohen et al. 2002; Dehaene et al. 2010; Pegado et al. 2011) whereas most of the studies favoring an interactive account of the vOT have used high-level reading tasks (e.g., lexical decision; Twomey et al. 2011; Woollams et al. 2011; Seghier and Price 2013).

Thus, the present fMRI study is aimed at investigating the involvement of the main regions along dorsal and ventral reading networks and the functional dynamics among these regions in late bilinguals as a function of the native versus non-native language (L1, L2), L2

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orthographic depth (transparent, opaque), and the demands of the reading task (perceptual, semantic). To do so, in line with previous neuroimaging studies, the reading tasks included words (orthographically legal pronounceable letter strings that have both semantic and phonological representations), pseudowords (orthographically legal pronounceable letter strings that have corresponding word-like phonological, but not semantic representations) and consonant strings (illegal non-pronounceable letter strings, lacking both semantic and phonological word-like associations; e.g., Petersen et al. 1990; Price et al. 1996). This stimuli manipulation allows examination of reading processes that typically rely on phonological computations carried out by regions along the dorsal stream, and on mapping orthographic-lexical stimuli onto semantic representations supported by regions along the ventral stream (Mechelli et al. 2003; Sandak et al. 2004; Schlaggar and McCandliss 2007).

Based on previous evidence, we expect that I) reading in L2, the later acquired language, will show stronger engagement of regions along the dorsal and ventral streams relative to reading in L1 (e.g., Wartenburger et al. 2003); II) regarding orthographic depth, whereas the group with a transparent L2 will exhibit greater reliance on regions along the dorsal (phonologically-tuned) pathway, the group with an opaque L2 will show stronger recruitment of ventral (lexico-semantic-tuned) regions (e.g., Das et al., 2011); III) with respect to task demands, we will specifically test if the left vOT will be similarly recruited across the semantic and perceptual reading tasks, which would support the prelexical computational hypothesis (e.g., Dehaene and Cohen 2011), or if task demands will modulate the engagement of left vOT, which would support the interactive account hypothesis (e.g., Price and Devlin 2011); IV) stimuli will modulate the engagement of reading networks, with dorsal regions subserving phonological processing more strongly recruited for pseudowords (which are assumed to lack semantic

information and rely on phonological representations) relative to words (e.g., Mechelli et al., 2003).

Additionally, we also expect that V) functional connectivity analyses will reveal different dynamics among dorsal and ventral regions during word reading in the same direction as the hypotheses mentioned above, with the exception that we expect to observe stronger functional coupling among regions for reading in L1 relative to reading in L2 due to a longer prior history of coactivations for reading in L1 in late bilinguals (Hebb 1949).

Methods

Participants

The final study sample consisted of 37 right-handed late bilinguals with Spanish as their L1 (mean age 29.10 ± 6.54; 22 females). All participants had normal or corrected-to-normal vision and no history of neurological or psychiatric disorders. The sample was divided into two groups of participants who have an L2 with either an opaque orthography (English; n = 19) or a transparent orthography (Basque; n =18). All subjects acquired the L2 after age 6 and were highly proficient in their L1 and L2, with minimal exposure to other languages (see Table 1).

Language proficiency was assessed using objective and subjective measures. An adaptation of the Boston Naming Test (Kaplan et al. 1983) in Basque, English and Spanish, controlling for cognates across these three languages, was used as an objective measure of vocabulary. Participants performed this picture-naming test, including 77 to-be-named drawings, in their respective two languages. They also filled in a language background questionnaire where they self-rated their proficiency levels in L1 and L2 and also rated the percentage of daily exposure to L1 and L2. Importantly, there were no differences between the groups in terms of

age, AoA of the L2, L1 and L2 proficiency measures, or in their overall daily exposure to L1 and L2 (all ps > .05). At the within-group level, while both objective and subjective measures indicated high proficiency in L1 and L2, proficiency and daily exposure were significantly higher in the L1 than in the L2 and age of acquisition was of course later in the L2 than in the L1 (ps > .001).

Table 1. Participants' demographics and linguistic characteristics by group. Standard deviations in parentheses.

	Spanish-Basque (n= 18)	Spanish-English (n = 19)	p values
Age (years)	31.0(7.8)	27.3(4.5)	p =.10
Gender (% female)	66.6	52.6	p =.38
Age of acquisition (years)			
L1	0	0	
L2	11.2 (7.1)	8.0 (2.1)	p =.09
Proficiency (correctly-named pictures)*			
L1	76.3 (1.3)	76.7 (0.7)	p =.41
L2	63.7 (10.0)	68.2 (7.6)	p =.15
Proficiency (self-rated)†			
L1	9.5 (0.7)	9.6 (0.6)	p =.80
L2	8.0 (0.9)	8.2 (0.8)	p =.42
Average daily exposure (%)§			
L1	68.1 (14.2)	72.2 (11.8)	p =.36
L2	22.5 (16.1)	26.6 (10.8)	p =.38

*Out of 77 pictures; § Average percentage across reading, writing, hearing, and speaking.
 p values corresponds to the t-test between groups, except for gender where a non-parameter chi-square test was used

Data from 1 additional participant were excluded from analysis due to excessive head motion during imaging (i.e., > 2 mm across the entire scan session). Prior to taking part in the experiment, all participants gave written informed consent in compliance with the ethical regulations established by the BCBL Ethics Committee and the guidelines of the Helsinki Declaration. Participants received monetary compensation for their participation.

Materials and Experimental Procedure

Participants carried out perceptual (low level) and semantic (high level) Go/No-Go tasks. In both tasks, subjects were visually presented with different character strings: words (e.g., *curtain*), pseudowords (e.g., *cinguda*), and consonant strings (e.g., *fstgklg*). Stimuli were visually presented in the center of the screen. During the perceptual task, participants were asked to press a button any time they saw a colored letter within a string (e.g., *brother*). In the semantic task, they were required to press a button when the word was the name of an animal (e.g., *turtle).*

The number of L1 (Spanish) stimuli presented within each task included 40 high-frequency words, 40 low-frequency words, 40 pseudowords, 40 consonant strings and 13% go trials. In the L2 (English or Basque), participants were presented with a similar number of stimuli and go trials per task as in the L1. Cognate words across languages were excluded to eliminate ambiguity. All words, between and within languages, were matched on frequency, number of orthographic neighbors and length (i.e., 5-8 characters). All pseudowords were created as a function of the selected words using Wuggy (Keuleers and Brysbaert 2010).

The study was administered in two separate sessions based on the language of the materials: L1 or L2. The order of these L1 or L2 sessions was counterbalanced across participants. However, to prevent participants generalizing the reading strategy used in the semantic task to the perceptual task within each of the language sessions, the perceptual task was always administered first, followed by the semantic task.

fMRI Data Acquisition

Whole-brain fMRI data acquisition was conducted on a 3-T Siemens TRIO whole-body MRI scanner (Siemens Medical Solutions, Erlangen, Germany) at the Basque Center on Cognition, Brain and Language (BCBL), using a 32-channel whole-head coil. Snugly fitting headphones (MR Confon, Magdeburg, Germany) were used to dampen background scanner noise and to enable communication with experimenters while in the scanner. Participants viewed stimuli back-projected onto a screen with a mirror mounted on the head coil. To limit head movement, the area between participants' heads and the coil was padded with foam and participants were asked to remain as still as possible.

In each session, functional images were acquired in four separate runs using a gradient-echo echo-planar pulse sequence with the following acquisition parameters: TR= 2000 ms, TE= 25 ms, 35 contiguous 3-mm axial slices, 0-mm inter-slice gap, flip angle = 90º, Field of view = 218 mm, 64 x 64 matrix Prior to each scan, four volumes were discarded to allow T1-Equilibration effects. High-resolution T1-weighted anatomical images were also collected. Within each functional run, the order of the study conditions (i.e., words, pseudowords, consonant strings, go trials) and the inter-trial intervals of variable duration corresponding to the MR frames that served as baseline or null events (i.e., fixation cross presented in the center of the screen, 30% of the total collected functional volumes) were determined with an algorithm designed to maximize the efficiency of the recovery of the blood oxygen level-dependent (BOLD) response (Optseq II; Dale 1999).

fMRI Data Analysis

Standard SPM8 (Wellcome Department of Cognitive Neurology, London) preprocessing routines and analysis methods were employed. Images were corrected for differences in timing of slice acquisition and were realigned to the first volume by means of rigid-body motion transformation. High-resolution anatomical T1 images and functional volumes were then co-registered and spatially normalized to T1 and echo-planar imaging templates, respectively, to enable anatomical localization of the activations. Templates were based on the MNI305 stereotaxic space (Cocosco et al., 1997), an approximation of Talairach space (Talairach and Tourneaux, 1988). The normalization algorithm used a 12-parameter affine transformation together with a nonlinear transformation involving cosine basis functions. During normalization, the volumes were sampled to 3-mm cubic voxels. Functional volumes were spatially smoothed with an 8-mm full width at half-maximum isotropic Gaussian kernel.

Statistical analyses were performed on individual participant data using the general linear model (GLM). fMRI time series data were modeled by a series of impulses convolved with a canonical hemodynamic response function (HRF). The motion parameters for translation (i.e., x, y, z) and rotation (i.e., yaw, pitch, roll) were included as covariates of noninterest in the GLM. Each trial was modeled as an event, time-locked to the onset of the presentation of each character string. The resulting functions were used as covariates in a GLM, along with a basic set of cosine functions that high-pass filtered the data, and a covariate for session effects. The least-squares parameter estimates of the height of the best-fitting canonical HRF for each study condition were used in pairwise contrasts. Contrast images from each subject were submitted to group analyses. At the group level, whole-brain contrasts between conditions were computed by performing one-sample *t* tests on these images, treating participants as a random effect. Brain coordinates

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throughout the text, as well as in tables and figures, are reported in MNI atlas space (Cocosco et al. 1997).

Region-of-interest (ROI) analyses were performed with the MARSBAR toolbox for use with SPM8 (Brett et al., 2002). Based on previous neuroimaging evidence, we functionally selected five left-lateralized regions, including *pars triangularis* (BA 45; center of mass = -48 27 14; volume = 9776), *pars orbitalis* (BA 47; center of mass = -40 30 -7; volume = 2160 mm^3), *pars opercularis* (BA 44; center of mass = -49 11 18; volume = 6184 mm^3), STG (BA 22; center of mass = -51 -44 7; volume = 783 mm^3) and inferior parietal cortex (IPC) (BA 40; center of mass = -30 -54 46; volume = 1984 mm^3). All these regions consisted of active voxels identified from the whole-brain contrast All > Null across all participants, $q < .001$ false discovery rate (FDR) corrected.

Given recent evidence emphasizing the strong inter-subject variability in the location of the left vOT region involved in reading (Glezer et al. 2009, 2013; Vogel et al. 2012), in the present study we identified the left vOT following three different criteria: 1) *literature ROI* (litROI) or ROI identified based on a prior meta-analysis of reading studies (Jobard et al. 2003), building a 5-mm radius ROI sphere centered at -44 -58 -15 MNI coordinates; 2) based on the *group activation* (gROIs), performing a whole-brain analysis across all participants for the contrast Words > Null ($q < .01$ FDR; masked with Words > Consonant Strings, $p < .05$ uncorrected) and identifying a) the highest T value within the fusiform gyrus (FG) and b) the highest T value within the FG closest to Cohen's VWFA definition (x = -43, y = -54, z = -12; Cohen et al. 2002) to build 5-mm radius sphere ROIs centered at those values; and 3) based on *individual ROIs* (iROIs), following the same approach described for the gROIs but identifying each of the local maximas to build the 5-mm radius sphere ROIs for each criteria at the

individual level and extracting the parameter estimates for each region at the single-subject level. The thresholding for these ROIs were Words > Null ($q < .05$ FDR; masked with Words > Consonant Strings, $p < .01$ uncorrected).

Thus, for the *gROI* and *iROI* approaches, masking the Word > Null contrast with Words > Consonant Strings allowed us to seek for activations in the left vOT that were related to identifying series of familiar strings. Moreover, for the *gROI* and *iROI* approaches, we also sought to examine whether the manner in which the local maxima within the left vOT is selected can determine the pattern of observed results: a) highest T value within the FG; and, b) highest T value within the FG closest to Cohen's VWFA definition.

We assessed functional connectivity *via* the beta correlation method (Rissman et al., 2004), implemented in SPM8 with custom Matlab scripts. The canonical HRF in SPM was fit to each occurrence of each condition and the resulting parameter estimates (i.e., beta values) were sorted according to the study conditions to produce a condition-specific beta series for each voxel. Two different functional connectivity analyses were performed: 1) pairwise connectivity between regions of interest within the ventral and dorsal reading networks; and 2) whole-brain functional connectivity with a left vOT seed region.

First, for the pairwise analysis we calculated beta-series correlation values for each pair of ROIs, participant and condition. Since the correlation coefficient is inherently restricted to range from -1 to +1, an arc-hyperbolic tangent transform (Fisher 1921) was applied to these beta-series correlation values to make its null hypothesis sampling distribution approach that of the normal distribution. Then, with the aim of testing for dorsal versus ventral differences in functional connectivity strength as a function of our experimental design, these Fisher's Z normally distributed values were submitted to a mixed-model analysis of variance (ANOVA)

including Group (Spanish-English vs. Spanish-Basque) as a between-subjects factor and Network (ventral vs. dorsal), Language (L1 vs. L2), Task (perceptual vs. semantic) and Stimuli (words, pseudowords and consonant strings) as within-subject factors. The selected ROIs for these functional connectivity analyses included the previously-described left-lateralized regions identified at the group level (i.e., *pars orbitalis*, *triangularis*, *opercularis*, STG, IPC) and the individually identified left vOT iROIs based on the highest T value within the FG. To ensure that differences between dorsal and ventral networks dynamics were not determined by differences in the cluster size of the functionally defined ROIs, we used 5-mm radius spheres centered at the highest local maxima for all the ROIs.

Second, for the whole-brain functional connectivity analysis, the beta series associated with the left vOT litROI seed were correlated with voxels across the brain to produce beta correlation images. Contrasts between beta correlation images were also subjected to an arc-hyperbolic tangent transform to allow for statistical inference based on the correlation magnitudes. Group-level and two-sample t-tests were performed on the resulting subject contrast images to produce group correlation contrast maps.

Results

Behavioral and fMRI results

Participants responded to the go trials during the fMRI task with an overall percentage of 90.18%, indicating that they paid attention to the task. Both groups responded to the same go trials across conditions. We performed two separate one-way ANOVAs with Group (Spanish-Basque bilinguals, Spanish-English bilinguals) as the between-subjects factor, with accuracy and the average RTs on the in-scanner go trials as the dependent measures. These analyses did not

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reveal any effect of the factor Group either for accuracy, ($F(1, 34) = .74$, $p = .40$, $\eta_p^2 = .03$), or for the reaction time ($F(1, 34) = 1.13$, $p = .30$, $\eta_p^2 = .04$) measures.

To identify brain regions associated with reading processes across all participants and factors in the experimental fMRI design, we computed a whole-brain contrast for All trials > Null (see Figure 1*A*). Consistent with prior neuroimaging evidence (e.g., Lau et al. 2008), this contrast revealed the involvement of a predominantly left-lateralized set of regions including *pars triangularis (*BA 45), *pars orbitalis* (BA 47), *pars opercularis* (BA 44), STG (BA 22), IPC (BA 40), and vOT (BA 37).
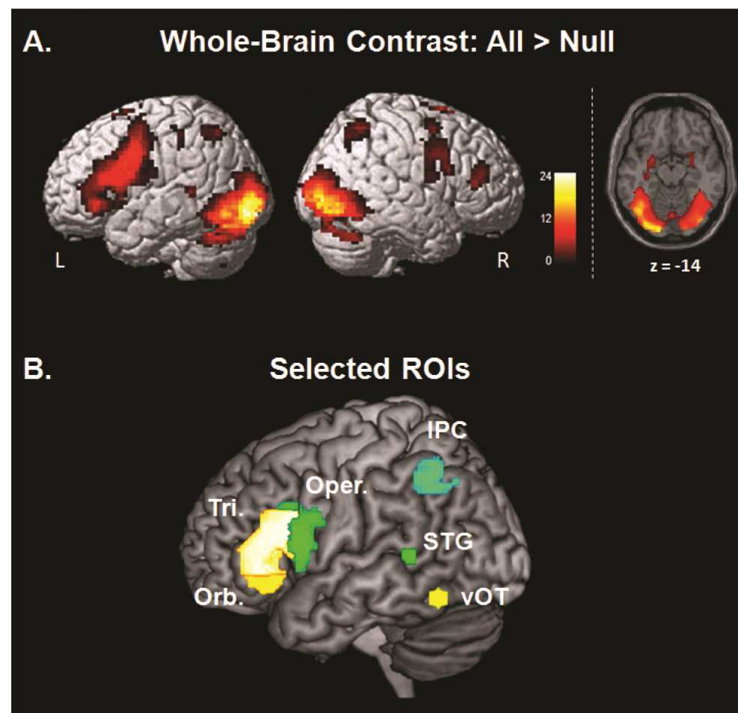

Figure 1. Brain renderings showing (*A*) activations for the All > Null whole-brain contrast across all subjects at a statistical threshold of q < .001 FDR-corrected and z-axis slice section for vOT cortex, and (*B*) location of the selected left-hemisphere ROIs within the ventral reading network (yellow shades), including *pars triangularis*, *pars orbitalis* and vOT, and within the dorsal reading network (green shades), including *pars opercularis*, STG y IPC for the dorsal reading network. Tri. = *pars triangularis*; Orb. = *pars orbitalis*; vOT = ventral occipitotemporal cortex; Oper. = *pars opercularis*; STG = superior temporal gyrus; IPC = inferior parietal cortex.

ROI analyses

We conducted ROI analyses to characterize the activation profile of regions of *a priori* interest for the main experimental conditions: Group (Spanish-English vs. Spanish-Basque), Language (L1 vs. L2), Task (perceptual vs. semantic), and Stimuli, (words, pseudowords and consonant strings). To avoid potential biases in the patterns of activation observed in these ROI analyses, these regions were selected from the general whole-brain All > Null contrast across all subjects, *q* < .001 FDR corrected, which yielded activations in most of the left-lateralized key regions involved in reading processes: IFG, posterior STG, inferior parietal cortex and vOT (see Figure 1*B*). Also, given the importance for the present study of the differential involvement of left IFG subregions in reading processes and evidence indicating that *pars opercularis* is part of the dorsal reading network and that *pars orbitalis* and *triangularis* are part of the ventral reading network, we sought to separately examine the pattern of activation within these IFG regions. Thus, we extracted fMRI parameter estimates from these ROIs and conducted hypothesis-driven analyses based on 2 (Group: Spanish-Basque, Spanish-English) X 2 (Language: L1, L2) X 2 (Task: perceptual, semantic) x 3 (Stimuli: words, pseudowords, consonant strings) mixed-model ANOVAs, with the last three factors varied within-subjects. Here, we just describe the ROI results for the higher order interactions specifically related to the main study hypotheses. Table 2 summarizes all the significant main and interactive effects that emerged in these analyses.

Table 2. Summary of the statistically significant effects observed in the ROI analyses of regions along the dorsal and ventral reading streams.

Region-of-interest (ROIs)	Coordinates (center of mass)			Main effects and interactions	*p values*
	x	**y**	**z**		
Dorsal-stream regions					
Left *pars opercularis* (BA 44)	-49	11	18	Group	$p < .05$
				Language	$p < .05$
				Stimuli	$p < .001$
				Group X Stimuli	$p < .01$
				Language X Stimuli	$p < .001$
				Task X Stimuli	$p < .01$
Left superior temporal gyrus (STG; BA 22)	-51	-44	7	Group	$p < .01$
				Language	$p < .05$
				Stimuli	$p < .001$
				Group X Stimuli	$p < .01$
				Language X Stimuli	$p < .01$
Left inferior parietal cortex (IPC; BA 40)	-30	-54	46	Language	$p < .001$
				Group X Stimuli	$p < .05$
Ventral-stream regions					
Left *pars triangularis* (BA 45)	-48	27	14	Stimuli	$p < .001$
				Language X Stimuli	$p < .05$
				Task X Stimuli	$p < .05$
Left *pars orbitalis* (BA 47)	-40	30	-7	Language	$p < .05$
				Stimuli	$p < .001$
				Language X Stimuli	$p < .01$
Left vOT (BA 37)*	-44	-58	-15	Language	$p < .01$
				Stimuli	$p < .001$
				Language X Stimuli	$p < .01$
				Task X Stimuli	$p < .01$

* Left vOT was localized using different approaches (i.e., litROI / groupROI/ iROI). Here the reported coordinates correspond to the litROI. Results were similar across the approaches used to define this region.

Dorsal regions

    Left pars opercularis. The ANOVA for this region revealed Group X Stimuli, ($F(2, 66) =$ 5.25, $p < .01$, $\eta_p^2 = .14$) and Language X Stimuli ($F(2, 66) = 11.30$, $p < .001$, $\eta_p^2 = .25$) statistically significant interactions (see Figure 2). Post-hoc analyses showed that the *Group X Stimuli* interaction was due to a stronger engagement of this region for pseudowords by the group with transparent L1 and L2 (i.e., Spanish-Basque) relative to the group with transparent L1 and opaque L2 (i.e., Spanish-English) ($p < .05$), in line with hypothesis II. With respect to the *Language X Stimuli* interaction, simple-effect analyses also revealed greater activation for L2 words than L1 words ($p < .001$), confirming hypothesis I. Also, consistent with our prediction (hypothesis IV), this region was more strongly engaged for pseudowords than words in L1 reading ($p < .001$).
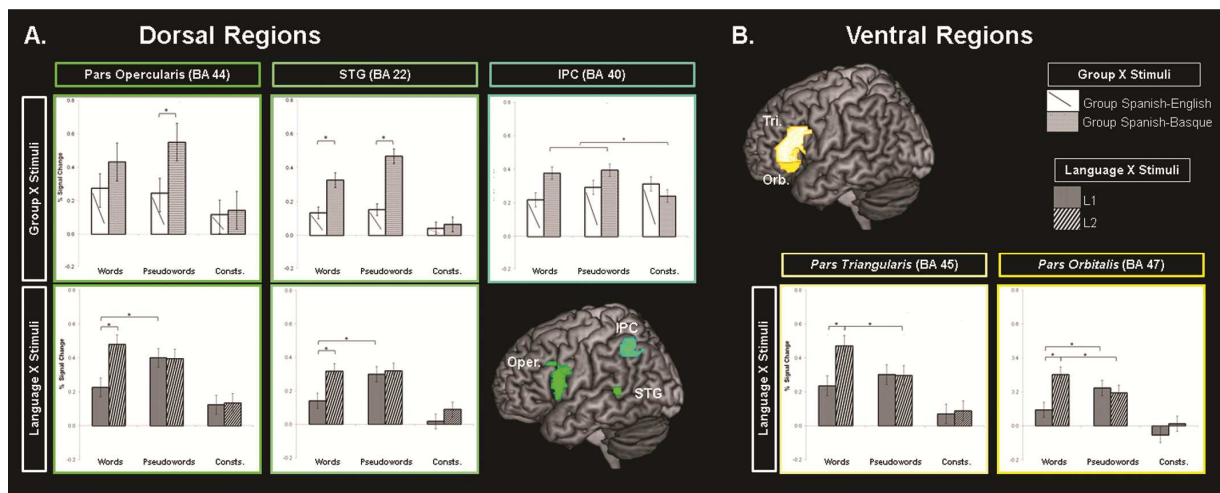

Figure 2. ROI analyses for left-lateralized regions within the dorsal and ventral reading network. A) Dorsal regions showed Group X Stimuli and Language X Stimuli interactions in *pars opercularis* (-49 11 18; BA 44) and STG (-51 -44 7; BA 22), and Group X Stimuli interaction in IPC (-30 -54 46; BA 40). B) Ventral regions within the left IFG, including *pars triangularis* (-48 27 14; BA 45) *pars orbitalis* (-40 30 -7; BA 47), showed Language X Stimuli interactions. Bar graphs show averaged parameter estimates (% signal change) for these interactions as a function of Group/Language and Stimuli. Asterisks within bar graphs indicate comparisons that showed statistically significant differences in % signal change (ps < .05). Consts. = consonant strings;

Oper. = *pars opercularis*; STG = superior temporal gyrus; IPC = inferior parietal cortex; Tri. = *pars triangularis*; Orb. = *pars orbitalis*.

Left STG. Results for this region revealed statistically significant Group X Stimuli ($F(2, 64) = 6.72$ $p < .01$, $\eta_p^2 = .17$) and Language X Stimuli ($F(2, 64) = 4.87$ $p < .01$, $\eta_p^2 = .13$) interactions (see Figure 2). Post-hoc comparisons for the *Group X Stimuli* interaction revealed that the group with transparent L1 and L2 (i.e., Spanish-Basque) showed a stronger activation for words and pseudowords than the Spanish-English group, where L1 is transparent and L2 is opaque ($p < .05$). Simple-effect analyses for the *Language X Stimuli* interaction showed greater activation for L2 words than L1 words, and no other significant difference between L1 and L2 for the other Stimuli conditions ($ps > .05$). Additionally, within the L1, pseudowords elicited higher activation than words ($p < .001$). These results are consistent with hypotheses I and II, and qualified our prediction of stronger engagement of this region for pesudowords relative to words, which was observed only for L1 reading (hypothesis IV).

Left IPC. The ANOVA for this region revealed a statistically significant *Group X Stimuli* interaction ($F(2, 58) = 3.60$, $p < .05$, $\eta_p^2 = .11$; Figure 2). Simple-effects analyses showed that, consistent with hypothesis II, this interaction was due to a stronger recruitment of this region for words and pseudowords than for consonant strings only in the group of Spanish-Basque bilinguals ($p < .05$).

Ventral regions

Left pars triangularis. ROI results for this region revealed a statistically significant *Language X Stimuli* ($F(2, 56) = 6.26$; $p < .05$, $\eta_p^2 = .18$) interaction. Simple-effect analyses revealed that this interaction was due to stronger activation for L2 words than L1 words ($p <$

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.001; Figure 2), in line with hypothesis I. In contrast, no differences between L1 and L2 were found for the other Stimuli conditions ($ps \geq .05$). Moreover, left *pars triangularis* was more strongly engaged for words than pseudowords in the L2 ($p < .01$). These differences were not observed in the L1 ($p = .20$).

Left pars orbitalis. The ANOVA for left *pars orbitalis* also showed a *Language X Stimuli* statistically significant interaction ($F(2, 46) = 5.76$; $p < .01$, $\eta_p^2 = .20$; see Figure 2). Simple-effect analyses revealed that this interaction was due to a stronger recruitment of this region for words in the L2 relative to words in the L1 ($p < .001$), confirming hypothesis I. No other stimuli conditions showed differential engagement for L2 vs. L1. Also, L2 words showed greater activation than L2 pseudowords ($p < .01$). In contrast, the L1 pseudowords elicited greater activation than L1 words ($p < .01$).

Left vOT. Due to recent evidence emphasizing the strong inter-subject variability in the location of the left vOT (Glezer et al. 2009, 2013), here we used three different criteria to identify this region: 1) *litROI*; 2) *gROIs*, identifying the a) highest T value within the FG and the b) highest T value within the FG closest to Cohen's VWFA definition (Cohen et al. 2002); and, 3) iROIs, following the same approach described for the *gROIs* but identifying each of the local maxima to build the ROIs at the individual level and extracting the parameter estimates for each region at the single subject level (see *Methods* section for further details).

The ANOVA carried out for the *litROI* revealed statistically significant Language X Stimuli ($F(2, 62) = 6.29$, $p < .01$, $\eta_p^2 = .17$) and Task X Stimuli ($F(2, 62) = 5.50$, $p < .01$, $\eta_p^2 = .15$) interactions (Figure 3). Post-hoc analyses for the *Language X Stimuli* interaction revealed that this region was more strongly engaged for words and consonant strings in L2 than in L1 ($ps < .05$), in line with hypothesis I. This Language effect was not observed for pseudowords.

Additionally, L1 pseudowords recruited this region more strongly than L1 words ($p < .01$); an effect that was not present in L2 ($p = .30$).

Regarding the *Task X Stimuli* interaction, this left vOT *litROI* showed the Task effect[1], or stronger activation for words in the semantic-task than in the perceptual-task ($p < .001$), in line with hypothesis III. This effect was not observed for pseudowords and consonant strings ($p = .20$). Moreover, words also showed higher activation than consonant strings only in the semantic-task ($p < .001$), an effect that was not observed in the perceptual task ($p = .60$).

Four separate ANOVAs for the *gROIs* and *iROIs* identified based on the highest T value within the FG and on the highest T value within the FG closest to Cohen's VWFA definition were also conducted. In line with what we observed in the *litROI* analysis, in all these ANOVAs interactions involving Language X Stimuli ($F(2, 60) \geq 4.10$, $ps < .05$, $\eta_p^2 \geq .10$) and Task X Stimuli ($F(2,60) \geq 6.50$, $ps < .05$, $\eta_p^2 \geq .17$) emerged.

To test for potential differences between these two ROI definitions and the selection of their local maxima, we carried out two separate 2 (ROI approach: *gROIs* vs. *iROIs*) X 2 (Local maxima selection: highest T value vs. highest T value closest to Cohen's VWFA) repeated measures ANOVAs, one for the language effect (i.e., activation for L2 words minus activation for L1 words) and one for the task effect (i.e., activation for words in the semantic task minus activation for words in the perceptual task). These analyses revealed no statistically significant main effects or interactions for the ROI approach and Local maxima selection factors for the language effect ($F(1, 28) \leq 4.22$, $ps \geq .05$, $\eta_p^2 \leq .13$), or for the task effect analyses ($F(1, 28) \leq 1.35$, $ps \geq .26$, $\eta_p^2 \leq .05$). Figure 3 shows ROI activations for *gROIs* and *iROIs* where local

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[1] This Task effect for word reading also emerged in left *pars opercularis* and *triangularis* ROIs (see Table 2). As indicated at the beginning of the *ROI Analyses* section, here we just describe the higher order interactions related to our main hypotheses and, therefore, results related to task demands are restricted to analysis involving the left vOT.

maxima were selected based on the highest T value within the FG, at the group or at the individual level, respectively. Thus, regional activation of the left vOT was modulated by language and task effects. These results were consistently confirmed across the different criteria used to identify this region, in line with hypotheses I and III.
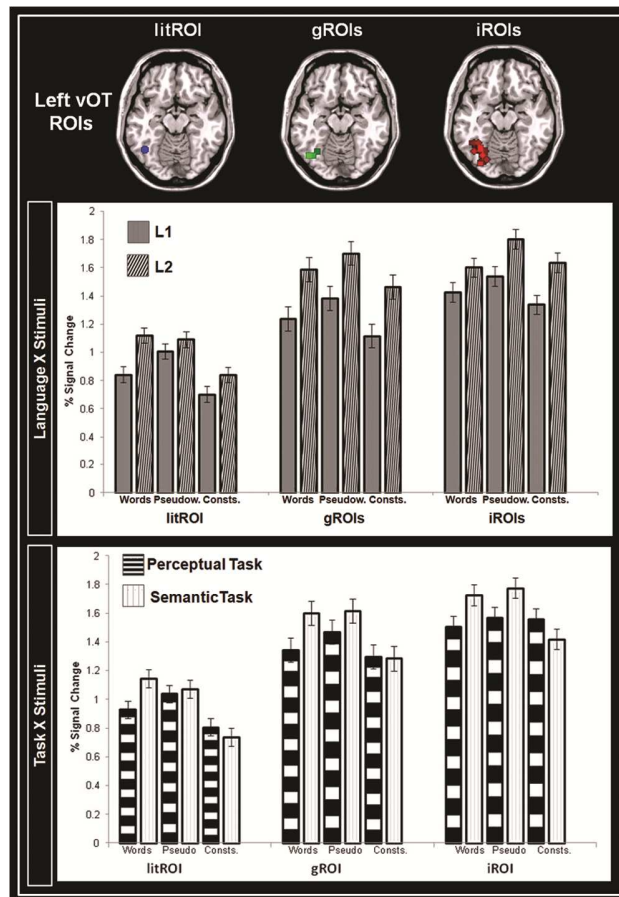

Figure 3. Left vOT ROI analyses based on three different approaches: Literature-based ROI (litROI), group-based ROIs (gROIs), and individually defined ROIs (iROIs). Bar graphs show averaged parameter estimates (% signal change) for these three left vOT ROI definitions as a function of Language/Task and Stimuli. For gROIs and iROIs the bar graphs show results for ROIs where local maximas were selected based on the highest T value within the FG, at the group or at the individual level, respectively. Pseudow. = pseudowords; Consts. = consonant strings.

Functional connectivity within dorsal and ventral reading networks

Here, we sought to investigate differences in temporal coupling between nodes within the main dorsal and ventral reading networks as a function of Group (Spanish-English vs. Spanish-Basque), Language (L1 vs. L2), Task (perceptual vs. semantic), and Stimuli (words, pseudowords and consonant strings). To do so, we used the beta-series correlation method (Rissman et al., 2004), building 5-mm-radius spheres centered at the highest local maxima within the previously-described left-lateralized ROIs (see *Methods* section for further details).

Fisher z-score transformed beta-series correlation values between all nodes within the ventral (*pars triangularis*, *pars orbitalis*, vOT) and dorsal (*pars opercularis*, STG, IPC) reading networks (Figure 4*A*) for each condition in our experimental design were averaged and submitted to mixed-model ANOVAs including Group (Spanish-English vs. Spanish-Basque) as a between-subjects factor and Network (ventral vs. dorsal), Language (L1 vs. L2), and Task (perceptual vs. semantic) as within-subject factors. Based on prior evidence supporting differential involvement of these reading networks as a function of stimuli type, we carried out three separate ANOVAs for words, pseudowords and consonant strings[2]. The ANOVA for word stimuli revealed statistically significant Network X Language ($F(1, 35) = 4.19$, $p < .05$, $\eta_p^2 = .11$), and Network X Task ($F(1, 35) = 8.88$, $p < .01$, $\eta_p^2 = .20$) interactions. In contrast, these interactions did not emerge for the pseudowords ($F(1, 35) \leq 1.01$, $ps \geq .30$, $\eta_p^2 \leq .03$) or the consonant strings ($F(1, 34) \leq 1.30$, $ps \geq .26$, $\eta_p^2 \leq .04$).

Post-hoc analyses for the Network X Language interaction for word stimuli revealed a statistically significant decrease in the strength of functional coupling in the dorsal network for

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[2] We also conducted the full ANOVA including Stimuli as a within-subject factor. This analysis revealed Network X Language X Stimuli ($F(2, 68) = 4.42$, $p < .05$, $\eta_p^2 = .12$), and Network X Task X Stimuli ($F(2, 68) = 7.07$, $p < .01$, $\eta_p^2 = .17$) as the highest order interactions. These results also support carrying out separate ANOVAs for each stimuli type.

reading words in L2 relative to L1 ($p < .001$; see Figure 4*A.1*). This effect was not observed in the ventral network, which showed similar connectivity strength for word reading in the L1 and L2 ($p = .10$). The Network X Task interaction for word stimuli was due to a statistically significant increase in the coupling strength between nodes within the ventral network for the semantic task relative to the perceptual task ($p < .01$; Figure 4*A.2*). This Task effect was not observed in the dorsal network ($p = .75$). Thus, whereas functional connectivity between regions within the dorsal network was modulated by Language, showing stronger coupling for reading words in L1 than in L2, functional connectivity between regions within the ventral network was modulated by Task demands, with stronger coupling observed for the semantic than for the perceptual task.

These results confirmed and qualified our prediction (hypothesis V), showing a stronger functional coupling for L1 relative to L2 only in the dorsal network and stronger connectivity among regions along the ventral network for semantic versus perceptual word reading.
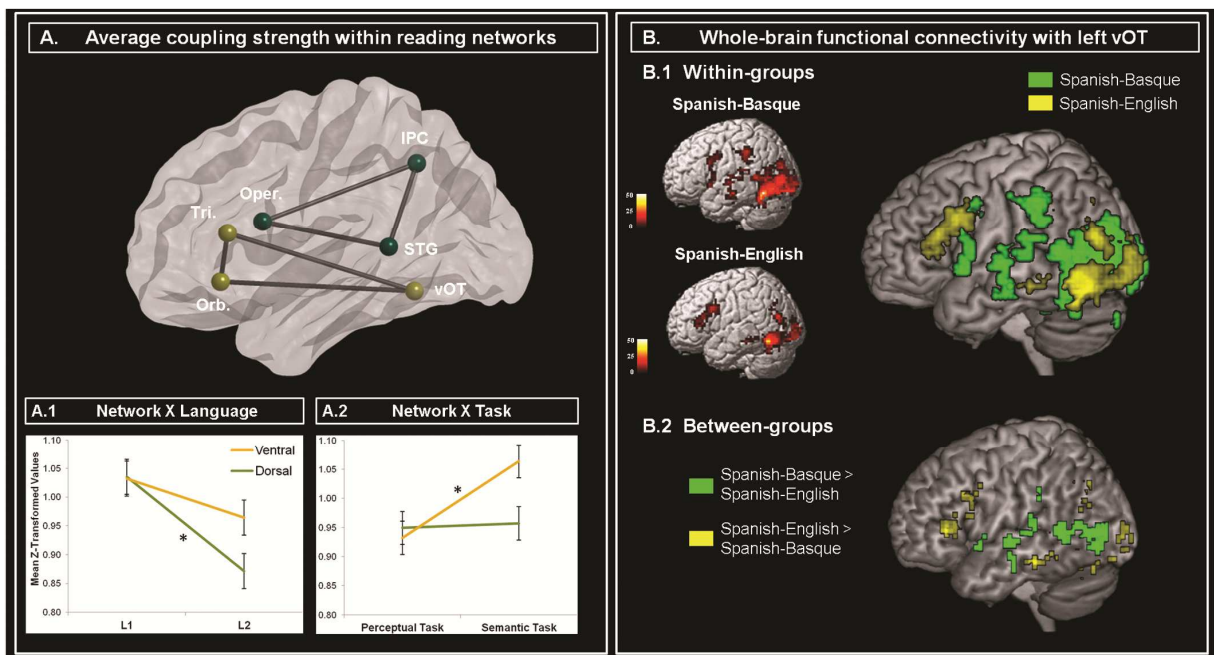
Figure 4. Functional connectivity analyses for ventral and dorsal reading networks. (A) A schematic sagittal view of the regions within dorsal (green) and ventral (yellow) reading networks and the pairwise connections among them that were submitted to functional connectivity analyses. All nodes correspond to 5-mm radius spheres centered at the highest local maxima for left-lateralized regions identified at the group level (i.e., *pars orbitalis*, *triangularis*, *opercularis*, STG, IPC) and at the individual level (iROIs) for the left vOT, based on the highest T value within the FG. Line graphs show average coupling strength (i.e., mean z-transformed values of the beta-series correlation) for processing word stimuli for the (A.1) Network X Language and (A.2) Network X Task interactions. Asterisks indicate comparisons that showed statistically significant differences in average strength of functional connectivity (*p*s < .05). (B) Left-hemisphere brain renderings showing whole-brain functional connectivity maps with left vOT for the contrast Words > Null (B.1) separately for the Spanish-Basque (in green) and Spanish-English (in yellow) groups at a FDR-corrected statistical threshold of $q < .0001$ (top panel) and (B.2) between-group Spanish-Basque > Spanish-English (in green) and Spanish-English > Spanish-Basque (in yellow) comparisons at a FDR-corrected statistical threshold of $q < .05$ (bottom panel). Tri. = *pars triangularis*; Orb. = *pars orbitalis*; vOT = ventral occipitotemporal cortex; Oper. = *pars opercularis*; STG = superior temporal gyrus; IPC = inferior parietal cortex.

Whole-brain functional connectivity with left vOT

The implementation of additional phonological and semantic processes supporting reading in transparent and opaque orthographies (e.g., Paulesu et al. 2000) depends upon initial stages of visual word recognition thought to be carried out by left vOT (Twomey et al. 2011). Therefore, we sought to use whole-brain functional connectivity methods to identify brain regions that were recruited in concert with left vOT during word reading as a function of L2 orthographic depth. To do so, the beta series associated with the left vOT litROI were correlated with voxels across the brain to produce beta correlation images. Group-level t-tests were performed on the resulting subject contrast images to produce group correlation contrast maps for reading words relative to baseline, separately for the group of bilinguals with a transparent L2 (i.e., Spanish-Basque) and for the group with an opaque L2 (i.e., Spanish-English) at a statistical threshold of $q < .0001$ FDR-corrected.

The analysis for the group with a transparent L2 revealed coactivations extending

anteriorly from left vOT to lateral temporal cortex (57 voxels in superior temporal gyrus, BA 22;

26 voxels in middle temporal gyrus, BA 21), as well as coactivated clusters in left parietal cortex

(76 voxels in IPC, BA 40; 30 voxels in supramarginal gyrus, BA 40), IFG (37 voxels in *pars*

opercularis, BA 44) and middle frontal gyrus (10 voxels, BA 9/46; see Figure 4*B.1*). In contrast,

the analysis for the group with an opaque L2 revealed extended coactivations anteriorly from the

left vOT to posterior lateral temporal cortex (37 voxels in middle temporal gyrus, BA 21; 35

voxels in inferior temporal gyrus, BA 22), as well as coactivated clusters in left IFG (81 voxels

in *pars triangularis*, BA 45) and middle frontal gyrus (23 voxels, BA 9/46). Thus, as expected,

whereas regions along the dorsal reading network showed tight coupling with left vOT for the

group with a transparent L2, regions along the ventral reading network were strongly coactivated

with left vOT for the group with an opaque L2. Importantly, this pattern of coupling dynamics

with left vOT as a function of L2 orthographic depth also holds for the contrast involving reading

L2 words versus resting baseline (at a slightly lower statistical threshold of $q < .005$ FDR-

corrected due to the lower number of observations in this analysis) but this was not the case for

the contrast involving reading L1 words versus baseline. These results strongly support our

predictions (hypothesis V, in line with hypothesis II), showing a clearly segregated profile of

coactivations during L2 word reading along the dorsal pathway for the group with a transparent

L2 and along the ventral pathway for the group with an opaque L2.

Finally, we conducted a two-sample t-test comparison for the whole-brain functional

connectivity with left vOT for reading words relative to baseline, which confirmed significant

between-group differences ($q < .05$ FDR-corrected) in the coupling strength of the left vOT with

regions along the dorsal stream for the comparison Spanish-Basque > Spanish-English and along

the ventral reading pathway for the comparison Spanish-English > Spanish-Basque (Figure *4B.2*).

Discussion

The present study aimed to investigate bilingual reading and the contributions of the native versus non-native language (L1, L2), L2 orthographic depth (transparent, opaque), task demands (perceptual, semantic) and stimuli type (words, pseudowords, consonant strings) to the regional activation and functional connectivity of areas within dorsal and ventral reading networks. To this end, we tested two groups of late bilinguals matched in terms of their L1 and L2 proficiency levels, daily exposure to their L1 and L2, age of acquisition of their L2 and minimal exposure to other languages, and differentiated in terms of the orthographic depth of their L2 (transparent vs opaque).

Our findings support a division of labor between ventral and dorsal reading networks in bilingual reading. In line with our main hypotheses, we found evidence from both regional and functional connectivity analyses indicating 1) effects of the native versus non-native language (i.e., factor Language: L1 vs. L2) with stronger recruitment of regions for word reading in L2 relative to L1, as well as stronger pairwise functional coactivation among regions within the dorsal reading network for word reading in L1 versus L2; 2) L2 orthographic depth (i.e., factor Group: Spanish-Basque vs. Spanish-English) was associated with differential engagement of areas along the dorsal pathway across languages and task demands, being more strongly engaged for participants in the Spanish-Basque group than for participants in the Spanish-English group, as well as stronger whole-brain functional connectivity during L2 word reading between the left vOT and the dorsal regions for the group with a transparent L2 and between the left vOT and ventral regions for the group with an opaque L2; 3) semantic reading demands relative to

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perceptual reading demands (i.e., factor Task: semantic vs. perceptual) elicited stronger recruitment of the left vOT across the several methodological approaches used to identify this region, as well as stronger pairwise functional connectivity between regions within the ventral reading network; and, 4) stronger activation for pseudowords relative to words (i.e., factor Stimuli: words, pseudowords, consonant strings) in left *pars opercularis* and left STG dorsal regions during L1 reading, in line with evidence showing the involvement of dorsal stream regions on reading processes that rely on phonological computations. These main findings are discussed below in four sections related to the main hypotheses and factors manipulated in the study: Language being read (i.e., Language), L2 orthographic depth (i.e., Group), task demands (i.e., Task), and stimuli type (i.e., Stimuli). Hypothesis V (relating to functional connectivity) is discussed throughout the four sections whenever the findings from the functional connectivity analysis are relevant to the factor in question.

Language effects (L2 > L1) across ventral and dorsal regions and strengthened coupling within the dorsal stream for L1 reading

L1 and L2 word reading differentially activated regions across both ventral and dorsal streams. As predicted by hypothesis I, all IFG regions, STG, and vOT showed greater regional activation for reading words in L2 than in L1. This effect is thought to be determined by the increased effort required to read in L2 in late bilinguals (Yetkin et al. 1996; Wartenburger et al. 2003) and is consistent with the linguistic profile of our participants, whose L2 proficiency level is high but still lower than their L1 proficiency. Regarding the effects on left vOT of the language used to read, previous reading studies with monolingual samples suggested that activation in this region can be tuned by language experience (Xue et al. 2006; Song et al. 2010;

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Xue et al. 2010). Our results suggest that this also seems to be the case in late bilinguals who showed stronger left vOT engagement for reading words in the L2 relative to the L1 across all the ROI approaches used to identify this region.

Our functional connectivity results support and qualify inferences from the regional activation data regarding language effects, in line with hypothesis V. Functional co-activation between regions within dorsal and ventral networks was similar for L1 word reading, but it decreased significantly for L2 relative to L1 in the dorsal stream. Stronger coactivation for L1 relative to L2 reading can be explained based on the prior history of coactivation among these brain regions, in line with a Hebbian-like learning rule (Hebb 1949; Harmelech et al. 2013). This is especially plausible for a cognitive function such as reading that we train on a daily basis and for comparisons involving L1 versus L2 in late bilinguals. Nevertheless, our data showed that this difference in the coactivation among regions for reading words in L2 relative to L1 was only statistically significant in the dorsal stream.

Prior research suggests that L2 is acquired through the same neural pathways responsible for L1 acquisition (Perani and Abutalebi 2005). According to Pugh et al.'s (2001) brain model of reading, when new words are read they are initially assigned to the dorsal pathway for the correct integration of semantic, orthographical, lexical and phonological processes. Then, once they are learnt, words are mainly read by means of the ventral pathway for rapid word identification, which is the main process involved in reading. Thus, the use of the available neural scaffolding from the L1 may contribute to making reading in L2 less dependent on the specific computations carried out between all the nodes within the dorsal network.

L2 Orthographic depth modulates regional activation and functional connectivity along the dorsal and ventral reading networks

Consistent with hypothesis II, all regions along the dorsal pathway showed greater activation for the group with a transparent L2 relative to the group with an opaque L2. Neuroimaging studies on reading have previously suggested that the activation in the dorsal areas examined here is strongly related to phonological processing (Buchsbaum and D'Esposito 2008; Graves et al. 2008). Specifically, the IPC has been previously linked to the phonological loop (Paulesu et al. 1993). In fact, in prior studies using bilingual samples, second-language phonological contrast has also shown parietal cortex engagement (Callan et al. 2003; Das et al. 2011). With respect to the STG, Meschyan and Hernández (2006) found that this region was more strongly engaged for reading in a transparent (Spanish) than in an opaque orthography (English). However, this finding included both the effects of language transparency and native versus non-native language, since Meschyan and Hernández's (2006) study included only one group of participants with a transparent L1 and an opaque L2. In the present study, we varied the orthographic depth of the L2 between groups, while controlling for proficiency and language (L1, L2) exposure. Our results of stronger engagement of dorsal regions for the group with both transparent languages (i.e., Spanish-Basque) reflect the sensitivity of regions within this network to sublexical orthography-to-phonology conversions, probably due to the more consistent grapheme-to-phoneme mapping of orthographically transparent languages (Paulesu et al. 2000).

Nevertheless, it is important to note that results of the present study did not fully support our hypothesis II in regard to stronger engagement of regions along the ventral network for the group with an opaque L2 compared to the group with a transparent L2. Having a group with mixed (transparent and opaque) orthographies might reduce the sensitivity of the design to

capture this regional modulation in the engagement of areas along the ventral network. Prior studies testing monolinguals with either an opaque or a transparent L1 suggest that this may indeed be the case (e.g., Paulesu et al., 2000).

Given previous evidence suggesting that orthographic depth has an impact on the semantic and phonological computations needed for successful reading (e.g., Das et al., 2011) and that the left vOT is a critical hub for visual word recognition (e.g., Twomey et al. 2011), we considered that the left vOT may be a critical region to observe differential functional dynamics with ventral and dorsal reading networks. Thus, in line with hypothesis V and in contrast to the connectivity analysis circumscribed to the functional coupling within each of the reading networks, we conducted whole-brain connectivity analysis using the left vOT as a seed to examine the profile of functional coactivation based on L2 orthographic depth. This analysis revealed strikingly distinct profiles in the coupling of left vOT with regions along the ventral network in the group with an opaque L2, on the one hand, and with regions along the dorsal network for the group with a transparent L2, on the other. Importantly, these results were observed during word reading, with further analysis indicating that this pattern of coactivation with left vOT holds for word reading in L2, but not for word reading in L1.

These findings are consistent with evidence suggesting that transparent orthographies with strong letter-to-sound mapping rely more on dorsal regions and that opaque orthographies rely more on lexico-semantic processes carried out by regions along the ventral pathway (Paulesu 2000; Das et al. 2011). Moreover, the present evidence highlights the importance of examining not only functional connectivity among the main nodes within the reading networks, but also with the left vOT.

Semantic reading demands elicit stronger left vOT engagement and functional connectivity among regions within the ventral stream.

Within the ventral stream, special attention was paid in the present study to the left vOT. It has been suggested that this region is involved in processing prelexical representations of visual word forms (Dehaene et al. 2002). However, other views have challenged this interpretation, based on evidence indicating that left vOT also participates in top-down predictions mediated by feedback connections interacting with bottom-up sensory inputs (Price and Devlin, 2011; see also Carreiras et al. 2014). To further unravel to what extent this region is sensitive to task-related modulations in bilinguals, in line with hypothesis III, we manipulated reading demands in our fMRI experimental design. To our knowledge, this is the first study to examine in bilinguals whether the activation profile of the vOT differs as a function of perceptual versus semantic reading tasks using a within-subject manipulation. Moreover, based on recent evidence (Glezer et al. 2009; 2013), here we sought to examine the regional activation of the vOT attending to different criteria to identify the area: coordinates from a prior meta-analysis and activation at the group and individual subject levels. It has been suggested that there is a strong inter-subject variability in the location of this region, probably due to its rapid re-adaptation to support a phylogenetically new skill (Dehaene and Cohen 2007; Bouhali et al. 2014). This variability may have given rise to the mixed results and interpretations put forward in previous studies in regard to the putative role of this region in reading (Glezer et al. 2013).

Importantly, across the different approaches used in the present study to identify the left vOT (i.e., litROI, gROIs and iROIs), our results consistently revealed that task effects modulated its pattern of regional activation. Since experimental stimuli were carefully matched across both tasks, this effect cannot be due to purely prelexical computation processes. Modulation of vOT

activation by reading demands suggests that this region integrates bottom-up with higher order information in line with the interactive account (Devlin et al. 2006; Price and Devlin 2011). Moreover, the consistency of the effects observed in left vOT across the different localization strategies used here provide strong evidence that these findings are not a mere topographic artifact.

Finally, in line with hypothesis V and previous evidence highlighting the role of the ventral reading stream in semantic processing, we observed stronger coupling among nodes within the ventral network for word reading under semantic versus perceptual demands. A remaining open question is to what extent using a reading task that further taxes phonological computations, such as a rhyming reading task (e.g., Booth et al., 2006; Cao et al., 2013), would yield stronger coupling among nodes within the dorsal network relative to a semantic reading task. Future neuroimaging research on bilingual reading should further characterize the impact of reading demands on the dynamics of ventral and dorsal reading pathways.

Stronger engagement of pseudowords versus words in dorsal regions for L1 reading

The language used to read (L1, L2) interacted with stimuli types, revealing relevant results for comparisons involving words and pseudowords in regions along the dorsal network. *Pars opercularis* and STG were more strongly recruited for pseudowords than words in L1 reading, while this effect was not present in L2 reading. The *pars opercularis* and STG are known for their involvement in phonological decoding (Zatorre et al. 1992; Simos et al. 2002). As pseudowords have no stored semantic representations, they may activate phonological processes more strongly because the phonological associations are less readily retrieved (Price et al. 1996). Thus, greater engagement of these regions for pseudowords likely reflects phonological decoding

or examining the correspondence between graphemes and phonemes to compute word and pseudoword pronunciation.

Additionally, stronger engagement for pseudowords than words during L1 reading was observed in *pars orbitalis*. Extensive evidence has linked *pars orbitalis* with increasing demands on semantic retrieval in the context of conflict (e.g., Badre and Wagner 2007; Ye and Zhou 2009; Nosarti et al. 2010). Pseudowords may also heavily recruit related semantic representations because of a more prolonged search for the missing meaning (Mechelli et al. 2003). The fact that this effect in the *pars opercularis*, STG and *pars orbitalis* was only present in L1 reading may be due to further attempts to phonologically decode and retrieve representations in the native language. Although there is prior evidence showing higher activation for pseudowords than words in these regions (Hagoort et al. 1999; Burton et al. 2005), this is the first study showing that this effect is present in L1 but not in L2 reading. These results partially confirmed, and qualified, hypothesis IV.

These findings have implications for the teaching of reading in a second language and for second language acquisition generally, in line with studies that have stressed the importance of taking into account languages' specificities, such as orthographic depth (e.g., Ziegler et al., 2010), in educational reading practices (e.g., Share, 2008). In transparent languages, most letters represent one sound and, therefore, it is easier to stress letter-sound conversion rules when teaching transparent L1 and L2 languages. Conversely, this strategy might not be the most optimal for learning to read in opaque languages, where the same letter can be associated with more than one sound, especially when individuals with a transparent L1 are taught to read in an opaque L2. Our findings also have implications for current theories and debates within the field of the neurobiology of language, paving the road for further examinations of functional

interactions among dorsal and ventral reading networks in samples with different language profiles.

Conclusion

Regional and functional connectivity data revealed a division of labor between dorsal and ventral reading networks in a sample of late Spanish-Basque and Spanish-English bilinguals, both groups matched in their proficiency and daily exposure to L1 and L2. Although reading in L1 and L2 appears to rely on the same neural networks, we observed stronger overall regional activation for L2 versus L1 reading and stronger coupling among dorsal regions for L1 versus L2 word reading, suggesting that L2 reading is supported by the preexisting L1 architecture but is more dependent on regional computations and less dependent on the processes carried out by the dorsal stream. L2 orthographic depth was associated with strikingly differentiated profiles of left vOT coactivation with dorsal regions for the group with a transparent L2 and with ventral regions for the group with an opaque L2. This indicates that the left vOT is critical to further evince differential functional coactivations involved in phonological and semantic computations required for successful L2 word reading as function of language orthography. Results from the task demand manipulation (semantic versus perceptual reading) supported the interactive account of left vOT and revealed that reading for meaning led to stronger coactivation between regions within the ventral network. The present study provides novel insights into how the bilingual brain reads, a matter of growing theoretical and applied interest, especially given that bilingualism is increasingly common in today's world.

Conflict-of-interest statement

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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References

Badre D, Wagner AD. 2007. Left ventrolateral prefrontal cortex and the cognitive control of memory. Neuropsychologia. 45:2883-2901.

Booth JR, Lu D, Burman DD, Chou TL, Jin Z, Peng DL, Zhang L, Ding GS, Deng Y, Liu L. 2006. Specialization of phonological and semantic processing in Chinese word reading. Brain Res. 1071:1 97-207.

Bouhali F, Thiebaut de Schotten M, Pinel P, Poupon C, Mangin JF, Dehaene S, Cohen L. 2014. Anatomical connections of the visual word form area. J Neurosci. 34:15402-15414.

Brett M, Anton JL, Valabregue R, Poline JB. 2002. Region of interest analysis using an SPM toolbox. Paper presented at the 8th International Conference on Functional Mapping of the Human Brain, Sendai, Japan, June 2–6.

Buchsbaum BR, D'Esposito M. 2008. The search for the phonological store: from loop to convolution. J Cogn Neurosci. 20:762-778.

Burton MW, Locasto PC, Krebs-Noble D, Gullapalli RP. 2005. A systematic investigation of the functional neuroanatomy of auditory and visual phonological processing. NeuroImage. 26:647-661.

Callan DE, Tajima K, Callan AM, Kubo R, Masaki S, Akahane-Yamada R. 2003. Learning-induced neural plasticity associated with improved identification performance after training of a difficult second-language phonetic contrast. NeuroImage. 19:113-124.

Cao F, Tao R, Liu L, Perfetti CA, Booth JR. 2013. High proficiency in a second language is characterized by greater involvement of the first language network: Evidence from Chinese learners of English. J Cogn Neurosci. 25:1649-1663.

Carreiras M, Armstrong BC, Perea M, Frost R. 2014. The what, when, where, and how of visual word recognition. Trends Cogn Sci. 18:90-98.

Carreiras M, Seghier ML, Baquero S, Estevez A, Lozano A, Devlin JT, Price CJ. 2009. An anatomical signature for literacy. Nature. 461:983-986.

Cocosco CA, Kollokian V, Kwan RKS, Evans AC. 1997. *BrainWeb: Online Interface to a 3D MRI Simulated Brain Database.* NeuroImage. 5:S425.

Cohen L, Dehaene S, Naccache L, Lehericy S, Dehaene-Lambertz G, Henaff MA, Michel F. 2000. The visual word form area: spatial and temporal characterization of an initial stage of reading in normal subjects and posterior split-brain patients. Brain. 123 Pt 2.:291-307.

Cohen L, Lehericy S, Chochon F, Lemer C, Rivaud S, Dehaene S. 2002. Language-specific tuning of visual cortex? Functional properties of the Visual Word Form Area. Brain. 125:1054-1069.

Dale AM. 1999. Optimal experimental design for event-related fMRI. Hum Brain Mapp. 8:109-114.

Das T, Padakannaya P, Pugh KR, Singh NC. 2011. Neuroimaging reveals dual routes to reading in simultaneous proficient readers of two orthographies. NeuroImage. 54:1476-1487.

Dehaene S, Cohen L. 2007. Cultural recycling of cortical maps. Neuron. 56: 384–398.

Dehaene S, Cohen L. 2011. The unique role of the visual word form area in reading. Trends Cogn Sci. 15:254-262.

Dehaene S, Le Clec HG, Poline JB, Le Bihan D, Cohen L. 2002. The visual word form area: a prelexical representation of visual words in the fusiform gyrus. Neuroreport. 13:321-325.

Dehaene S, Nakamura K, Jobert A, Kuroki C, Ogawa S, Cohen L. 2010. Why do children make mirror errors in reading? Neural correlates of mirror invariance in the visual word form area. NeuroImage. 49:1837-1848.

Devlin JT, Jamison HL, Gonnerman LM, Matthews PM. 2006. The role of the posterior fusiform gyrus in reading. J Cogn Neurosci. 18:911-922.

Fisher, RA. 1921. *On the probable error of a coefficient of correlation deduced from a small sample.* Metron. 1:3-32.

Friederici AD. 2009. Pathways to language: fiber tracts in the human brain. Trends Cogn Sci. 13:175-181.

Friederici AD. 2012. The cortical language circuit: from auditory perception to sentence comprehension. Trends Cogn Sci. 16:262-268.

Glezer LS, Jiang X, Riesenhuber M. 2009. Evidence for highly selective neuronal tuning to whole words in the "visual word form area". Neuron. 62:199-204.

Glezer LS, Riesenhuber M. 2013. Individual variability in location impacts orthographic selectivity in the "visual word form area". J Neurosci. 33:11221-11226.

Graves WW, Grabowski TJ, Mehta S, Gupta P. 2008. The left posterior superior temporal gyrus participates specifically in accessing lexical phonology. J Cogn Neurosci. 20:1698-1710.

Grosjean 2010. Bilingual: Life and reality: Harvard University Press.

Hagoort P, Indefrey P, Brown C, Herzog H, Steinmetz H, Seitz RJ. 1999. The neural circuitry involved in the reading of German words and pseudowords: A PET study. J Cogn Neurosci. 11:383-398.

Harmelech T, Preminger S, Wertman E, Malach, R. 2013. The day-after effect: long-term, hebbian-like restructuring of resting-state fMRI patterns induced by a single epoch of cortical activation. J Neurosci. 33:9488-9497.

Hebb DO. 1949. The organization of behavior: a neuropsychological theory. New York: Psychology Press.

Jamal NI, Piche AW, Napoliello EM, Perfetti CA, Eden GF. 2012. Neural basis of single-word reading in Spanish-English bilinguals. Hum Brain Mapp. 33:235-245.

Jobard G, Crivello F, Tzourio-Mazoyer N. 2003. Evaluation of the dual route theory of reading: a metanalysis of 35 neuroimaging studies. NeuroImage. 20:693-712.

Kaplan, Harold, Weintraub. 1983. Boston Naming Test. Philadelphia: Lea & Febiger

Keuleers E, Brysbaert M 2010. Wuggy: a multilingual pseudoword generator. Behav Res Methods. 42:627-633.

Lau EF, Phillips C, Poeppel D. 2008. A cortical network for semantics: de.constructing the N400. Nat Rev Neurosci. 9:920-933.

Mechelli A, Gorno-Tempini ML, Price CJ. 2003. Neuroimaging studies of word and pseudoword reading: consistencies, inconsistencies, and limitations. J Cogn Neurosci. 15:260-271.

Meschyan G. Hernandez AE. 2006. Impact of language proficiency and orthographic transparency on bilingual word reading: An fMRI investigation. NeuroImage. 29:1135-1140.

Nosarti C, Mechelli A, Green DW, Price CJ. 2010. The impact of second language learning on semantic and nonsemantic first language reading. Cereb Cortex. 20:315-327.

Paulesu E, Fazio F, Menoncello L, Brunswick N, Cappa SF, Cotteli M, Cossu G, Corte F, Lorusso M, Pesenti S, Gallagher A, Perani D, Price C, Frith CD, Frith U. 2000. A cultural effect on brain function. Nature. 3:91-96.

Paulesu E, Frith CD, Frackowiak RS. 1993. The neural correlates of the verbal component of working memory. Nature. 362:342-345.

Pegado F, Nakamura K, Cohen L, Dehaene S. 2011. Breaking the symmetry: mirror discrimination for single letters but not for pictures in the Visual Word Form Area. NeuroImage. 55:742-749.

Perani D, Abutalebi J 2005. The neural basis of first and second language processing. Curr Opin Neurobiol. 15:202-206.

Perani D, Abutalebi J, Paulesu E, Brambati S, Scifo P, Cappa SF, Fazio F. 2003. The role of age of acquisition and language usage in early, high-proficient bilinguals: an fMRI study during verbal fluency. Hum Brain Mapp. 19:170-182.

Petersen SE, Fox PT, Snyder AZ, Raichle ME. 1990. Activation of extrastriate and frontal cortical areas by word and word-like stimuli. Science. 249:1041-1044.

Price CJ, Devlin JT. 2011. The interactive account of ventral occipitotemporal contributions to reading. Trends Cogn Sci. 15:246-253.

Price CJ, McCrory E, Noppeney U, Mechelli A, Moore CJ, Biggio N, Devlin JT. 2006. How reading differs from object naming at the neuronal level. NeuroImage. 29:643-648.

Price CJ, Wise RJS, Frackowiak RS. 1996. Demonstrating the Implicit processing of visually presented words and pseudowords. Cereb Cortex. 6:62-70.

Pugh KR, Mencl WE, Jenner AR, Katz L, Frost SJ, Lee JR, Shaywitz SE, Shaywitz BA. 2001. Neurobiological studies of reading and reading disability. J Commun Disord. 34:479-492.

Rissman J, Gazzaley A, D'Esposito M. 2004. Measuring functional connectivity during distinct stages of a cognitive task. NeuroImage. 23:752-763.

Rolheiser T, Stamatakis EA, Tyler LK. 2011. Dynamic processing in the human language system: synergy between the arcuate fascicle and extreme capsule. J Neurosci. 31:16949-16957.

Rueckl JG, Paz-Alonso PM, Molfese PJ, Kuo WJ, Bick A, Frost SJ, Hancock R, Wu DH, Mencl WE, Duñabeitia JA, Lee JR, Oliver M, Zevin JD, Hoeft F, Carreiras M, Tzeng OJL, Pugh KR, Frost, R. 2015. Universal brain signature of proficient reading: Evidence from four contrasting languages. Proc Natl Acad Sci USA. 112:15510-15515.

Sandak R, Mencl WE, Frost SJ, Rueckl JG, Katz L, Moore DL, Mason SA, Fulbright RK, Constable RT, Pugh KR. 2004. The neurobiology of adaptive learning in reading: a contrast of different training conditions. Cogn Affect Behav Neurosci. 4:67-88.

Saur D, Kreher BW, Schnell S, Kummerer D, Kellmeyer P, Vry MS, Umarova R, Musso M, Glauche V, Abel S, Huber W, Rijntjes M, Hennig J, Weiller C. 2008. Ventral and dorsal pathways for language. Proc Natl Acad Sci USA. 105:18035-18040.

Schlaggar BL, McCandliss BD. 2007. Development of neural systems for reading. Annu Rev Neurosci. 30:475-503.

Seghier ML, Price CJ. 2013. Dissociating frontal regions that co-lateralize with different ventral occipitotemporal regions during word processing. Brain Lang. 126:133-140.

Share DL. 2008. On the Anglocentricities of current reading research and practice: The perils of overreliance on an "outlier" orthography. Psychol Bull. 134:584-615.

Simos PG, Fletcher JM, Foorman BR, Francis DJ, Castillo EM, Davis RN, Fitzgerald M, Mathes PG, Denton C, Papanicolaou AC. 2002. Brain activation profiles during the early stages of reading acquisition. J Child Neurol. 17:159-163.

Song Y, Bu Y, Hu S, Luo Y, Liu J. 2010. Short-term language experience shapes the plasticity of the visual word form area. Brain Res. 1316:83-91.

Talairach J, Tournoux P. 1988. Co-planar stereotaxic atlas of the human brain. Stuttgart, Germany: Thieme Verlag.

Twomey T, Kawabata Duncan KJ, Price CJ, Devlin JT. 2011. Top-down modulation of ventral occipito-temporal responses during visual word recognition. NeuroImage. 55:1242-1251.

Wartenburger I, Heekeren RH, Abutalebi J, Cappa SF, Villringer A, Perani D. 2003. Early setting of grammatical processing in the bilingual brain. Neuron. 37:159-170.

Woollams AM, Silani G, Okada K, Patterson K, Price CJ. 2011. Word or word-like? Dissociating orthographic typicality from lexicality in the left occipito-temporal cortex. J Cogn Neurosci. 23:992-1002.

Vogel AC, Petersen SE, Schlaggar BL. 2012. The left occipitotemporal cortex does not show preferential activity for words. Cereb cortex. 22:2715-2732.

Xue G, Chen C, Jin Z, Dong Q. 2006. Language experience shapes fusiform activation when processing a logographic artificial language: an fMRI training study. NeuroImage. 31:1315-1326.

Xue G, Mei L, Chen C, Lu ZL, Poldrack RA, Dong Q. 2010. Facilitating memory for novel characters by reducing neural repetition suppression in the left fusiform cortex. PLoS One. 5:e13204.

Ye Z, Zhou X. 2009. Conflict control during sentence comprehension: fMRI evidence. NeuroImage. 48:280-290.

Yetkin O, Yetkin FZ, Haughton VM, Cox RW. 1996. Use of functional MR to map language in multilingual volunteers. Am J Neuroradiol. 17:473-477.

Zatorre RJ, Evans AC, Meyer E, Gjedde A. 1992. Lateralization of phonetic and pitch discrimination in speech processing. Science. 256:846-849.

Ziegler JC, Bertrand D, Tóth D, Csépe V, Reis A, Faísca L, Saine N, Lyytinen H, Vaessen A, Blomert L. 2010. Orthographic depth and its impact on universal predictors of reading a cross-language investigation. Psychol Sci, 21:551-559.