Full Length Articles

Neural activation in speech production and reading aloud in native and non-native languages

Jonathan A. Berken [a,b,*], Vincent L. Gracco [b,d], Jen-Kai Chen [a], Kate E. Watkins [c], Shari Baum [b], Megan Callahan [a,b], Denise Klein [a,b]

[a] Cognitive Neuroscience Unit, Montreal Neurological Institute, Montreal, QC, Canada
[b] Centre for Research on Brain, Language, and Music, McGill University, Montreal, QC, Canada
[c] Department of Experimental Psychology, University of Oxford, Oxford, UK
[d] Haskins Laboratories, New Haven, CT, USA

ARTICLE INFO

ABSTRACT

We used fMRI to investigate neural activation in reading aloud in bilinguals differing in age of acquisition. Three groups were compared: French–English bilinguals who acquired two languages from birth (simultaneous), French–English bilinguals who learned their L2 after the age of 5 years (sequential), and English-speaking monolinguals. While the bilingual groups contrasted in age of acquisition, they were matched for language proficiency, although sequential bilinguals produced speech with a less native-like accent in their L2 than in their L1. Simultaneous bilinguals activated similar brain regions to an equivalent degree when reading in their two languages. In contrast, sequential bilinguals more strongly activated areas related to speech-motor control and orthographic to phonological mapping, the left inferior frontal gyrus, left premotor cortex, and left fusiform gyrus, when reading aloud in L2 compared to L1. In addition, the activity in these regions showed a significant positive correlation with age of acquisition. The results provide evidence for the engagement of overlapping neural substrates for processing two languages when acquired in native context from birth. However, it appears that the maturation of certain brain regions for both speech production and phonological encoding is limited by a sensitive period for L2 acquisition regardless of language proficiency.

Introduction

The capacity of the brain to comprehend and produce two languages with distinct phonological, syntactic, and semantic properties is a testament to its plasticity. The degree to which competence in specific language functions can be attained may be limited by age of acquisition (AoA) and the extent to which the first language (L1) has been established when the second language (L2) is learned (Hatzidaki et al., 2011; Nosarti et al., 2010; Klein et al., 2006; Tan et al., 2003; Flege et al., 1999; Lenneberg, 1967). These limitations may reflect a critical period (Lenneberg, 1967) due to normal time-sensitive maturational changes in the brain (Bialystok, 1997; Long, 1990). As is true for other types of learned skills, not all facets of L2 proficiency (i.e., phonological, syntactic, and semantic) are likely to reflect the same temporal

constraints. The optimal window for phonological learning, in fact, may begin to close prior to one year of age (Kuhl, 2010; Werker and Lalonde, 1988; Werker and Tees, 1984).

Developmental studies have suggested that the ability of an infant raised in a monolingual environment to discriminate the phonetic signatures of different languages begins to wane after six months of life (Kuhl, 2010; Werker and Lalonde, 1988; Werker and Tees, 1984). In contrast, infants exposed to two languages simultaneously from birth continue to discriminate the phonetic representations of each (Burns et al., 2007), indicating that the timeline for the shift from language-general to language-specific processing extends longer for such children (Werker and Byers-Heinlein, 2008). In addition, it has been observed that individuals learning two languages simultaneously from birth (simultaneous bilinguals) speak with a native-like accent in both languages, compared to sequential bilinguals who learned their second language after acquiring their first, despite considerable effort, years of practice, and competence in other aspects of language production (Reiterer et al., 2011; Johnson and Newport, 1989). Indeed, only about one in ten bilinguals acquiring an L2 as an adult can expect to produce speech without a foreign accent in the non-native language (Golestani and Zatorre, 2004, 2009; Golestani et al., 2007; Birdsong, 1999, 2005).

* Corresponding author at: Cognitive Neuroscience Unit, Montreal Neurological Institute, 3801 University Street, Room 264, Montréal, Québec H3A 2B4, Canada. Fax: +1 514 398 1338.
E-mail address: jonathan.berken@gmail.com (J.A. Berken).

While much of the neuroimaging literature on bilingual language processing has focused on disentangling the relative effects of AoA from proficiency (e.g., Perani et al., 1998), differences between simultaneous and sequential bilinguals have received limited attention. Of note are studies reporting increased neural activation for late-learning bilinguals relative to monolingual controls in regions involved in speech production (Frenck-Mestre et al., 2005; Klein et al., 1994, 1995) and more recent structural neuroimaging data showing late-learning bilinguals with increased cortical thickness in the left inferior frontal gyrus (IFG) compared to simultaneous bilinguals (Klein et al., 2014). These observations are consistent with a more robust recruitment of language-related brain areas for L2 compared to L1 to compensate for less efficient use of these regions in the second language (Indefrey, 2006). If, indeed, the sensitive period for developing phonology draws to a close in early infancy, then it seems probable that the loss of innate mechanisms for native-like pronunciation would result in greater activation during speech for sequential bilinguals, but not for simultaneous bilinguals.

Explanations as to how some bilinguals manage to accomplish native articulatory competence in a second language, while others do not, remain conjectural, although differences in psycholinguistic processes such as phonological working memory (Baddeley, 2003; Thorn and Gathercole, 2001; Gathercole et al., 1994, 1997) and in the neural activation associated with speech-motor planning and auditory–perceptual processing have been observed (Hu et al., 2013). While studies of proficient bilinguals suggest considerable convergence in the brain loci activated when speaking either language, there is evidence that the extent of activation can vary between L1 and L2 in certain regions, especially those involved in speech articulation (Parker Jones et al., 2012, 2013; Simmonds et al., 2011b; Klein et al., 1994, 1995, 2006; Frenck-Mestre et al., 2005).

Such studies, however, raise the question as to whether this difference in functional activity relates to language proficiency, AoA, or both (Parker Jones et al., 2012; Simmonds et al., 2011a,b). Wartenburger et al. (2003) used grammatical and semantic judgment tasks to disentangle the effects of AoA from proficiency on brain function in Italian–German bilinguals and suggested that the relative importance of these factors depended on the aspect of language examined. To date, however, few neuroimaging studies have investigated the relationship between AoA and phonological skill in a second language. Klein et al. (2006) compared L1 and L2 word repetition in late bilinguals and found greater activity for L2 in speech-motor areas, indicating the increased articulatory demands of pronouncing words in the non-native language. However, the late bilinguals included in that study were not tightly controlled for proficiency nor were they contrasted with an early or simultaneous bilingual group.

Here, we used fMRI to compare neural activation during French and English oral sentence reading in simultaneous bilinguals, sequential bilinguals, and L2-exposed monolinguals. Our bilingual subjects were matched for linguistic proficiency, but differed in native-like accent in L2. We observed similar functional activity for simultaneous bilinguals and monolinguals, but different patterns for sequential bilinguals, supporting the notion that compensatory mechanisms are recruited to achieve oral proficiency when sequential bilinguals read aloud in a late-learned language. The sequential bilinguals engaged brain regions more strongly in their L2 than in their L1, most notably in areas associated with orthographic to phonological mapping (e.g., occipital and occipitotemporal cortex Dehaene et al., 2010; McCandliss et al., 2003; Cohen et al., 2002) and articulatory motor planning (e.g., motor cortex, IFG, and cerebellum Indefrey, 2012; Fiez and Petersen, 1998; Bavelier et al., 1997). The results provide evidence for the engagement of overlapping neural substrates for processing two languages when acquired in native context from birth. However, it appears that the maturation of certain brain regions for both speech production and phonological encoding is limited by a sensitive period for L2 acquisition, regardless of language proficiency.

Materials and methods

Participants

Forty-seven right handed subjects differing in language experience were selected for this study: French–English simultaneous bilinguals who acquired two languages from birth, French (L1)–English (L2) sequential bilinguals who acquired their second language after the age of 5 years, and English monolinguals. Simultaneous bilinguals acquired both of their languages at home, while sequential bilinguals acquired their L2 at school. All bilinguals are exposed to and use French and English on a daily basis as self-reported on the Language Experience and Proficiency Questionnaire (LEAP-Q; Marian, 2007). Although monolinguals reported some daily exposure to French as a function of living in Montreal, they considered themselves solely speakers of the English language. As such, these individuals differ from monolinguals most commonly examined. To acknowledge this distinction, we describe our monolingual subjects as exposed to an L2.

All participants were healthy young adults, without hearing or reading impairment, neurological disorder, or history of brain trauma as assessed by a telephone interview prior to scanning. Multilinguals were excluded. Individuals self-reporting a high degree of musical expertise were also excluded, given that there is some suggestion of a correlation between musical skill and language ability (Christiner and Reiterer, 2013). Intelligence was assessed by the Block Design subtest of the Wechsler Abbreviated Scale of Intelligence (WASI) (Wechsler, 1981; see Table 1). Participants were recruited from the McGill community and gave informed consent. Testing procedures were approved by the Research Ethics Board of the Montreal Neurological Institute, McGill University.

Language assessment

Language competence was assessed with the Language Experience and Proficiency Questionnaire (Marian, 2007). Simultaneous and sequential bilinguals reported a high level of proficiency in both languages, while English-speaking monolinguals maintained a high proficiency in their native language only (see Table 2). Subjects rated their ability to learn a language since it has been shown that greater language learning aptitude is reflected structurally in the brain (Golestani et al., 2002, 2007; Golestani and Zatorre, 2004). Comparable degrees of self-assessed aptitude were obtained.

In addition, recordings were made of the participants producing speech and reading standardized paragraphs aloud in French and English. Participants were instructed to speak for 2 min in each language following simple open-ended prompts (i.e., *S'il vous plaît, décrivez une journée typique pour vous [à la plage/au zoo]. En utilisant un vocabulaire pertinent, vous pouvez vous rappeler d'une journée [à la plage/au zoo] ou créer des histoires qui fonctionnent dans le contexte; Please describe what could be a typical day for you at the [beach/zoo]. Using relevant vocabulary,*

Table 1
Background information on participant groups.

	Simultaneous bilingual	Sequential bilingual	Monolingual
	N = 16	N = 13	N = 18
Gender			
% Male	37	62	67
% Female	63	38	33
Mean age (years)	23.3 (3.1)	25.2 (4.2)	25.8 (4.5)
Mean L2 AoA (years)	1.0 (0.0)	13.9 (5.0)	N/A
% Daily exposure to French	60.0 (16.9)	40.0 (18.5)	15.7 (15.2)
% Daily exposure to English	40.0 (15.4)	60.0 (18.5)	84.3 (15.7)
Formal education (years)	16.1 (2.7)	17.1 (2.8)	16.6 (1.8)
Block Design Subtest, WASI (1–19)	13.6 (1.6)	13.5 (2.5)	13.3 (2.0)

Values are means (SD).

Table 2
Self-assessed language ability.

	Simultaneous bilingual		Sequential bilingual		Monolingual	
Language aptitude	6.7 (1.9)		6.8 (1.5)		5.6 (2.2)	
	French	English	French	English	French	English
Speaking ability	8.9 (1.2)	9.1 (1.1)	9.3 (.95)	7.5 (1.7)	1.6 (1.0)	9.6 (.51)
Listening comprehension	9.6 (.62)	9.6 (.89)	9.8 (.60)	8.2 (1.4)	1.8 (.99)	9.5 (.62)
Reading ability	9.4 (.51)	9.6 (.62)	9.5 (.66)	7.9 (1.3)	2.2 (.94)	9.5 (.71)

Scores are means (SD); rating scale (1 — very low, 10 — perfect).

you are welcome to recall or create stories that fit the description). Instructions were delivered in the language required for the response. Speech was evaluated for (a) lexicosemantics, (b) syntax, (c) speech fluency, and (d) phonology.

To quantify lexicosemantics, we examined the recorded samples for the number of unique and total words generated (Cobb, 2009). Sentences produced during spontaneous speech were categorized according to complexity of syntax. Sentences were characterized as: (i) simple, with a single declarative clause structure (e.g., The boy goes to the store); (ii) compound, with 2 declarative phrases joined by a conjunction (e.g., The girl went to the store because she needed vegetables); or, (iii) complex, where a sentence includes at least one subordinate/embedded clause (e.g., The house, that he painted, was green). Words per minute for French and English spontaneous speech were measured as an index of speech fluency (Cobb, 2009). To assess accent, 3 English and 3 French native speakers, unfamiliar with the study, evaluated recorded speech for the degree to which subjects sounded native-like (1 — very poor/très faible, 7 — native-like/langue maternelle). Results were averaged across raters within each language, which provided accent scores for each subject in both languages. Interrater reliability was high for both French and English raters (α = .92 and .80, respectively).

To evaluate reading ability, we selected English and French passages from a bank of short texts used extensively for neuropsychological testing at the Montreal Neurological Institute. These paragraphs were matched for word count and contained all of the phonemes of their respective languages. Subjects were evaluated for reading speed and number of errors made to assess reading skill.

Procedure

Blood Oxygen Level-Dependent (BOLD) fMRI scans were obtained while participants read sentences aloud in French and English. Blocks of French and English sentences were presented in a predetermined order on a back-projected screen that participants viewed through a mirror mounted on the head coil. Each sentence was presented for 7750 ms followed by the 2210 ms whole-brain acquisition. Subjects were instructed to read the sentences aloud at a normal pace and to stop talking when the scanner noise started. Only sentences produced within the silent period were analyzed.

For the baseline condition, strings of XXX that matched our meaningful sentences in structure, were presented to subjects to control for visual input. Participants were instructed to scan strings of XXX as if they were reading a sentence, but not to speak out loud. Subjects practiced the task outside of the scanner prior to testing. A total of 120 acquisitions per subject were acquired comprised of 48 English, 48 French, and 24 visual control sentences and were presented in blocks.

Stimuli

Meaningful French and English sentences comprised of an article, noun, verb [preposition if necessary], article, and noun were used. Nouns and verbs were selected from the medium and high frequency

lists (Masterson and Druks, 1998) and the CELEX lexical database (Baayen et al., 1995). Phrases were in the present or imperfect tense and were controlled for the number of syllables (French, average 8.0, range 6–10; English, average 7.8, range 6–10; [p = .095, ns]). French and English are languages with moderate orthographic depth, in that their spelling-sound correspondences are not highly consistent (Goswami, 2008; Ziegler and Goswami, 2005). Sentences were, therefore, constructed to minimize such irregularities. All sentences were constructed to follow the same format. Representative phrases for French included: *Le mari dansait avec sa femme, Ce garçon achète des souliers*. Representative phrases for English included: *An airplane flew over the village, The parrot bites his cookie*.

Data acquisition

Participants were scanned at the Montreal Neurological Institute on a 3 T Siemens Magnetom Trio A Tim System. For all subjects, high resolution T_1-weighted images were obtained as anatomical references using a 3D Magnetization Prepared Rapid Gradient Echo (MP-RAGE) sequence (TR = 2300 ms, TE = 2.98 ms, slice thickness = 1 mm, image matrix = 256 × 256, flip angle = 30°, FOV = 256 mm, interleaved excitation).

Functional images for the sentence reading tasks were acquired with T_2^*-weighted gradient echo (GE) echo-planar imaging (EPI) sequence (3.5 × 3.5 × 3.5 mm³ voxel size, flip angle = 90°, echo time = 30 ms, repetition time = 9960 ms, silent interval = 7790 ms, interleaved excitation) with 42 oblique slices (30° off the anterior–posterior commissural plane).

Subjects read the sentences aloud during the 7790 ms silent interval in order to eliminate motion-induced artifact, consistent with the sparse sampling methodology (Gracco et al., 2005). This permitted each participant's speech to be recorded without being masked by the scanner noise and with audible feedback and is important for reducing imaging artifacts induced by speech-related head movements. In-scanner speech was transduced with a high quality optical microphone (Sennheiser MO 2000) and digitized directly to disc for offline analysis.

Statistical analyses of fMRI data

Motion correction was first performed by realigning all functional volumes to the third volume of each run followed by spatial smoothing of the images with a 6 mm full-width-at-half-maximum Gaussian filter. A principal components analysis (PCA) was then carried out to reveal temporal and spatial drifts. Voxel-wise statistical analysis of the motion corrected fMRI time series was performed with fMRIstat (Worsley et al., 2002; www.math.mcgill.ca/keith/fmristat) based on a linear model with correlated errors. A design matrix of the linear model containing the onset time and duration of each task condition was convolved with a hemodynamic response function modeled as a difference of two gamma functions and adjusted to coincide with the acquisition of each slice. Spatial and temporal drifts identified from the PCA analysis were incorporated into the design matrix as confounds. In addition, speech production time for each sentence stimulus was included as a confound, to ensure that any observed activation was unrelated to individual differences in speech duration. For each participant, contrasts comparing activity during each condition were calculated using voxel-level t-statistics to identify brain regions that were engaged during each experimental task relative to baseline. The correlation structure was modeled as an autoregressive process of degree 1. At each voxel, the autocorrelation parameter was estimated from the least squares residuals using the Yule–Walker equations, after a bias correction for correlations induced by the linear model. The autocorrelation parameter was first regularized by spatial smoothing, then used to 'whiten' the data and the design matrix. The linear model was then re-estimated using least squares on the whitened data to produce estimates of effects and their standard errors. An average across participants was achieved

by first normalizing individual data through linear registration to the MNI template using an in-house algorithm (Collins et al., 1994). Normalized data were then combined using a mixed-effects linear model that involves smoothing a ratio of the variance of the random-effects to the variance of the fixed-effects. The amount of smoothing was chosen to achieve 100 effective degrees of freedom (Worsley et al., 2002).

Patterns of activation were first established for each group during French and English reading relative to the baseline. Four analyses were then performed to determine whether simultaneous bilinguals processed their two native languages in the same manner. We first conducted a conjunction analysis to identify the common brain areas recruited when simultaneous bilinguals read aloud in each L1, by using the test statistic images from the English and French conditions. These images were converted into p-values, which were used to determine the conjunction, the maximum of the p-values thresholded at $p < 0.05$. We then performed a within-group direct subtraction of overt sentence reading in French and English for the simultaneous bilinguals, a contrast of simultaneous bilinguals and monolinguals during English reading, and a contrast of simultaneous and sequential bilinguals during French reading.

We next examined the pattern of brain activation for sequential bilinguals in their second language, acquired later in development, yet mastered to a high degree of proficiency. Here, we contrasted the functional activation elicited during L2 reading with that during L1 reading. In addition, sequential bilinguals were contrasted with simultaneous bilinguals and monolinguals for their non-native English reading, to compare their activation patterns with two groups whose facility with English was considered native.

Threshold for significance was calculated using stat_threshold from the fMRIstat package. This functionality calculates both voxel-based as well as cluster thresholds using the minimum given by a Bonferroni correction and random field theory to correct for multiple comparisons, taking into account the non-isotropic spatial correlation of the errors (Worsley et al., 2002). Peak threshold was established at $t = 4.3$. By default, stat_threshold uses the cluster threshold of 3.17 ($p = 0.001$, uncorrected) for activation clusters greater than 222 mm^3 (equivalent to 28 voxels).

Finally, a whole-brain regression analysis was performed in all bilinguals (simultaneous and sequential) to determine those brain regions with activity that covaried with age of acquisition. Chronological age was included in the analysis as a co-variate of non-interest.

Identification of activated brain regions was determined by comparison with the Talairach atlas (Talairach and Tournoux, 1988).

Results

Quantitative language assessment

Simultaneous and sequential bilinguals were highly proficient in both languages, although sequential bilinguals produced speech with a more native-like accent in their L1 than L2 ($p = .002$). No other significant behavioral differences were noted. As expected, monolinguals were highly proficient only in English, their native language, and demonstrated a uniformly low ability in French ($p < .05$; see Table 3a).

In-scanner speech

French and English sentences recorded during scanning were analyzed by two-way ANOVA with 1 between (simultaneous bilingual, sequential bilingual, monolingual) and 1 within (French, English) subject factor for accuracy, onset time, and duration. Onset time, defined as the interval between the visual presentation of a stimulus and the onset of the spoken response, and utterance duration, were determined from acoustic recordings. Speech onset and offset for each sentence were established by visual inspection of the Praat analysis software generated spectrogram (Boersma, 2001). Following a significant interaction between group, language, and reading accuracy ($F(2,1) = 63.9$, $p < .0001$), post-hoc pairwise analyses were performed. Monolinguals were less accurate at reading in French than simultaneous and sequential bilinguals ($p = .0001$), and more accurate than sequential bilinguals when reading in English ($p = .006$). A significant interaction between group, language, and onset time was also observed ($F(2,1) = 16.1$, $p = .0001$). Here, sequential bilinguals took longer to begin reading in English than both simultaneous bilinguals ($p = .009$) and monolinguals ($p = .0001$), while monolinguals took longer than sequential bilinguals to begin reading in French ($p = .009$). Finally, a significant interaction between group, language, and sentence duration was determined ($F(2,1) = 56.2$, $p = .0001$). Monolinguals were found to read more slowly in French than in English ($p = .0001$), and more slowly than either bilingual group when reading in French ($p = .0001$; see Table 3b).

Within-group activation patterns during L1 and L2 sentence reading relative to visual baseline

Whole-brain analyses revealed similar functional activity during sentence reading in both languages for simultaneous and sequential bilinguals that included the bilateral motor cortex, anterior, mid, and

Table 3
Analysis of recorded speech and reading.

	Simultaneous bilingual		Sequential bilingual		Monolingual	
	French	English	French	English	French	English
a) Pre-scan samples						
Lexicosemantics						
No. of unique words	130.0 (22.4)	134.3 (15.2)	131.6 (26.4)	119.5 (28.9)	31.4 (11.6)	140.4 (21.1)
No. of total words	310.5 (71.6)	304.4 (41.8)	304.1 (63.9)	278.6 (64.2)	48.3 (22.1)	309.2 (65.5)
Syntax						
% Complex sentences	36.3 (14.7)	40.2 (14.8)	36.7 (17.5)	38.7 (18.1)	2.4 (6.1)	41.0 (14.4)
Speech fluency						
Words per minute	155.1 (35.9)	152.2 (20.9)	151.9 (31.8)	139.3 (32.1)	24.1 (11.0)	154.6 (32.8)
Phonology						
Accent (rating 1–7)	5.4 (1.1)	5.8 (.88)	5.9 (.95)	4.1 (1.5)	2.0 (.58)	5.8 (1.4)
Reading						
Reading time (s)	56.4 (7.5)	49.7 (5.2)	54.8 (7.4)	56.7 (12.6)	135.2 (42.3)	45.6 (5.0)
# Errors	1.3 (.86)	1.1 (.68)	.92 (.86)	1.8 (1.3)	12.4 (10.1)	.67 (.84)
b) In-scanner speech						
% Accuracy	96.6 (3.8)	95.6 (5.1)	97.8 (2.8)	88.8 (15.4)	40.7 (27.8)	99.1 (2.3)
Onset time (s)	1.23 (.25)	1.21 (.23)	1.46 (.27)	1.48 (.23)	1.22 (.21)	1.02 (.21)
Sentence duration (s)	1.99 (.22)	1.87 (.16)	2.07 (.29)	2.24 (.38)	3.25 (.82)	1.76 (.21)

Scores are means (SD).

posterior superior temporal gyrus, along with activation of the thalamus and cerebellum. When monolinguals read in their native language, English, they recruited the same brain regions as those activated by simultaneous and sequential bilinguals reading in their L1. As expected, when reading sentences in French, a language to which monolinguals had only passive exposure, they activated additional brain regions, including the pre-supplementary motor area, premotor cortex, the anterior portion of the insula, the inferior frontal cortex, the left fusiform gyrus, and bilateral regions of the occipital cortex (see Fig. 1 and Table 4).

Neural substrates of native language reading

The conjunction analysis confirmed the common activation of the primary motor cortex, superior temporal cortex, and cerebellum, during the French and English reading conditions for simultaneous bilinguals (see Table 5). No significant differences in brain activity were observed when simultaneous bilinguals read aloud in their two languages. A contrast of simultaneous bilinguals and English-speaking monolinguals during English sentence reading revealed no significant differences in activation, nor were significant differences in functional patterns observed in a comparison of simultaneous and sequential bilinguals reading in French.

Neural patterns of sentence reading in a non-native language

Sequential bilinguals, when reading aloud in L2 compared to L1, activated several brain regions more significantly, including the left premotor cortex, left inferior frontal gyrus, and left fusiform gyrus, as well as the bilateral pre-supplementary motor areas, right lateral inferior occipital cortex and cerebellar vermis (Fig. 2 and Table 6). In addition, sequential bilinguals activated some of the same left hemisphere regions as were found in the L2 > L1 comparison when contrasted with simultaneous bilinguals. Additional areas of activation included the thalamus and the right cingulate cortex. When compared to monolinguals, sequential bilinguals also activated more significantly the anterior temporal cortex and the left posterior cerebellum and regions in the thalamus (Fig. 3 and Table 7).

Regression analysis in bilinguals: positive correlation with age of acquisition

A significant, positive correlation between AoA and functional activity was noted in bilinguals in the inferior frontal gyrus, premotor cortex, cingulate cortex, fusiform gyrus, and occipital cortex. That is, the later the second language was acquired, the greater the activation was observed in these brain regions (Fig. 4 and Table 8).

Discussion

We used fMRI to investigate what occurs in the brain when individuals read aloud in native and non-native languages. To do this, three groups were compared: French–English simultaneous bilinguals who acquired two languages from birth, French–English sequential bilinguals who learned their L2 after the age of 5 years, and English-speaking monolinguals who were passively exposed to a second language, French. While our bilingual groups differed in AoA, they were matched for language proficiency, although sequential bilinguals
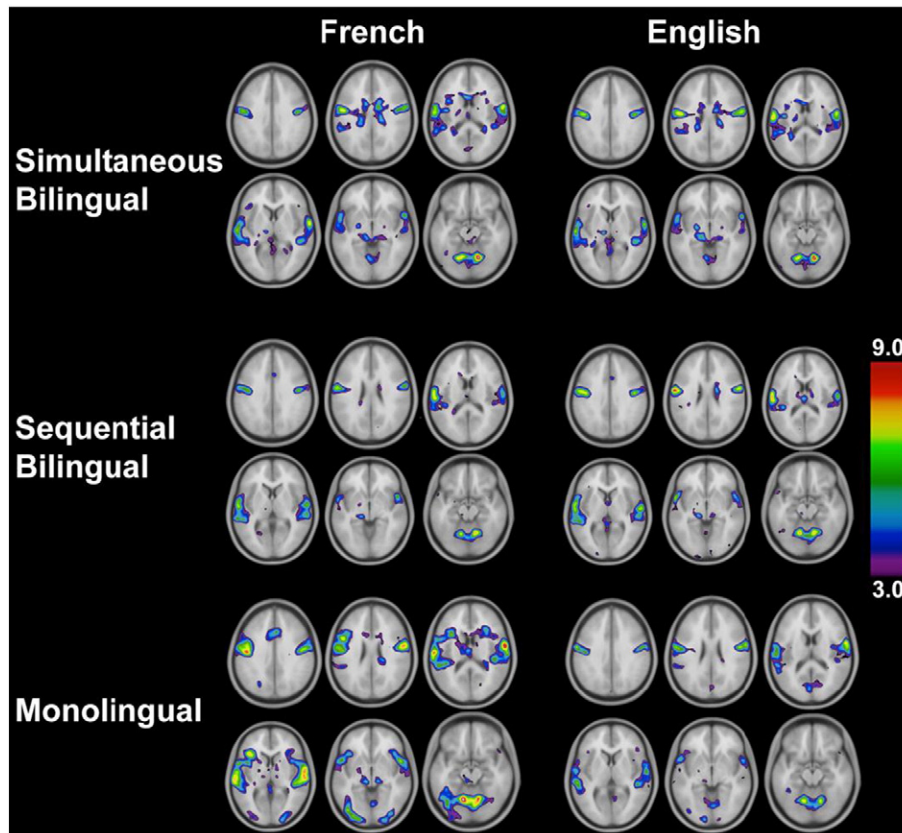

Fig. 1. Whole brain analyses of the three groups during overt sentence reading in French and English relative to visual baseline, revealed significant activation of motor and auditory regions bilaterally. While simultaneous and sequential bilinguals recruited similar brain regions when reading in both languages, English-speaking monolinguals activated additional brain areas when reading sentences in French that included the bilateral pre-supplementary motor areas, premotor cortex, the anterior portion of the insula, the inferior frontal cortex, the left fusiform gyrus, and bilateral regions of the occipital cortex. Six horizontal images are presented for each group for both languages at $z = 35, 25, 15, 5, -5,$ and -15. The left hemisphere is on the left side in all horizontal sections. Threshold for $p < .001$ uncorrected significance was established at $t = 4.3$ for the voxels and $t = 3.17$ for activation clusters greater than 222 mm^3 (equivalent to 28 voxels).

Table 4

Activation patterns for overt sentence reading in French and English relative to the visual baseline. x, medial–lateral distance relative to the midline (positive = right); y, anterior–posterior distance relative to the anterior commissure (positive = anterior); z is the superior–inferior distance relative to the anterior commissure line (posterior = superior). Threshold for $p < .001$ uncorrected significance was established at $t = 4.3$ for the voxels and $t = 3.17$ for activation clusters greater than 222 mm³ (equivalent to 28 voxels).

Brain area	Simultaneous bilinguals		Sequential bilinguals		Monolinguals	
	x, y, z	t	x, y, z	t	x, y, z,	t
French — baseline						
Left hemisphere						
Pre-supplementary motor area					−2, 10, 56	7.2
Frontal operculum					−38, 24, 4	7.7
Anterior insula					−32, 22, 4	6.6
Premotor cortex					−48, 10, 26	7.2
Primary motor cortex	−52, −6, 30	7.5	−44, −12, 38	6.3	−48, −12, 34	8.4
Anterior superior temporal gyrus	−58, 4, −4	5.7	−58, 2, 0	5.7	−56, 8, 2	7.0
Mid. superior temporal gyrus	−64, −14, 8	6.8	−62, −12, 8	7.5	−64, −24, 8	8.5
Post. superior temporal gyrus	−44, −40, 12	5.4	−63, −36, 8	6.5	−64, −24, 8	8.5
Globus pallidus	−22, −5, −8	4.8	−18, −5, −8	4.3	−22, −11, −1	4.7
Thalamus	−12, −26, −6	4.9	−14, −28, −6	4.9	−10, −16, 10	5.4
Anterior cerebellum	−20, −66, −14	7.3	−14, −62, −16	7.2	−14, −62, −18	9.7
Fusiform gyrus					−42, −76, −8	6.9
Occipital cortex					−22, −88, −6	6.1
Right hemisphere						
Pre-supplementary motor area					2, 16, 46	6.6
Frontal operculum					40, 28, −1	5.4
Anterior insula					32, 28, 2	4.8
Inferior frontal gyrus					54, 8, 0	6.6
Premotor cortex					62, −2, 16	8.9
Primary motor cortex	62, −2, 18	7.8	60, −4, 24	6.2	58, −4, 23	8.1
Anterior superior temporal gyrus	56, 10, −2	5.8	53, 10, −5	6.1	52, 10, −4	7.1
Mid. superior temporal gyrus	62, −16, 2	4.4	62, −10, 8	6.6	62, −6, 6	8.0
Post. superior temporal gyrus	52, −34, 8	6.0	64, −30, 8	5.7	56, −26, 8	7.0
Thalamus	8, −28, −8	4.9			12, −16, −10	4.3
Anterior cerebellum	16, −64, −14	8.7	18, −60, −18	8.0	16, −60, −18	9.3
Occipital cortex					34, −82, −4	5.9
					22, −96, 2	5.7
English — baseline						
Left hemisphere						
Inferior frontal gyrus	−40, 30, 1	3.6	−54, 12, 2	6.0		
Primary motor cortex	−52, 8, 28	7.8	−58, −6, 28	8.4	−60, −6, 35	6.6
Anterior superior temporal gyrus	−58, 6, −4	6.0	−58, 6, −3	6.6	−56, 11, −4	5.6
Mid. superior temporal gyrus	−62, −14, 8	6.9	−58, −14, 4	6.2	−60, −18, 10	5.3
Post. superior temporal gyrus	−62, −30, 2	4.7	−54, −36, 8	6.6	−56, −40, 10	6.5
Thalamus	−12, −18, 6	6.0	−14, −26, −6	5.3		
Anterior cerebellum	−14, −61, −18	8.2	−15, −62, −16	8.1	−17, −62, −18	6.9
Right hemisphere						
Primary motor cortex	60, −4, 18	7.4	58, −4, 26	7.2	54, −6, 28	6.7
Anterior superior temporal gyrus	58, 10, −5	5.9	62, −5, 0	5.3	58, 8, −4	4.9
Mid. superior temporal gyrus	62, −12, 2	4.6	64, −10, 10	7.2	62, −10, 8	6.5
Post. superior temporal gyrus	45, −36, 8	6.3	58, −26, 3	5.5	46, −34, 7	6.2
Anterior cerebellum	16, −62, −16	9.7	14, −62, −16	7.8	20, −62, −20	6.8

produced speech with a less native-like accent in their L2 than in their L1. This distinction, and the use of an overt reading paradigm, allowed us to tease out the effects of AoA on brain function, given that it has been shown that reading skill depends on phonological development (Goswami, 2008) and that the sensitive period for phonology begins

Table 5

Conjunction analysis of French and English sentence reading by simultaneous bilinguals. Thresholded at $p < 0.05$.

Brain area	x, y, z	p	Cluster volume (mm³)
Left hemisphere			
Primary motor cortex	−52, −8, 28	0.00010	3568
Anterior superior temporal gyrus	−58, 4, −4	0.04300	176
Posterior superior temporal gyrus	−62, −14, 14	0.00010	640
Anterior cerebellum	−16, −62, −18	0.00010	2112
Right hemisphere			
Primary motor cortex	60, −4, 18	0.00010	1952
Anterior temporal gyrus	62, −4, 10	0.00010	312
Posterior superior temporal gyrus	46, −36, 8	0.00600	792
Anterior cerebellum	16, −64, −16	0.00010	2120

to close early in infancy (Kuhl, 2010; Werker and Lalonde, 1988; Werker and Tees, 1984).

We had several hypotheses. First, we predicted that native French and native English speakers would activate similar regions (e.g., inferior frontal gyrus, motor cortex, basal ganglia, thalamus, and cerebellum) when processing speech in their L1, and that these areas would be among those identified in previous literature (e.g., Indefrey, 2012; Fiez and Petersen, 1998; Bavelier et al., 1997; for a review, see Price, 2012; Price, 2010). We also predicted that when a non-native language is acquired to a high degree of proficiency, speech-motor and reading-specific areas (e.g., occipital and occipitotemporal cortex (Dehaene et al., 2010; McCandliss et al., 2003; Cohen et al., 2002)) would be activated that are similar to those recruited in the L1 reading condition, but to a greater extent as a consequence of L2 having been learned after an optimal period. We also predicted that because simultaneous bilinguals and monolinguals acquired speech in their native languages within the sensitive period for language development, they would not have to enlist extra resources.

Our findings were in agreement with our predictions. Native speakers showed similar functional activation regardless of whether their L1 was French or English, in regions that were distributed across
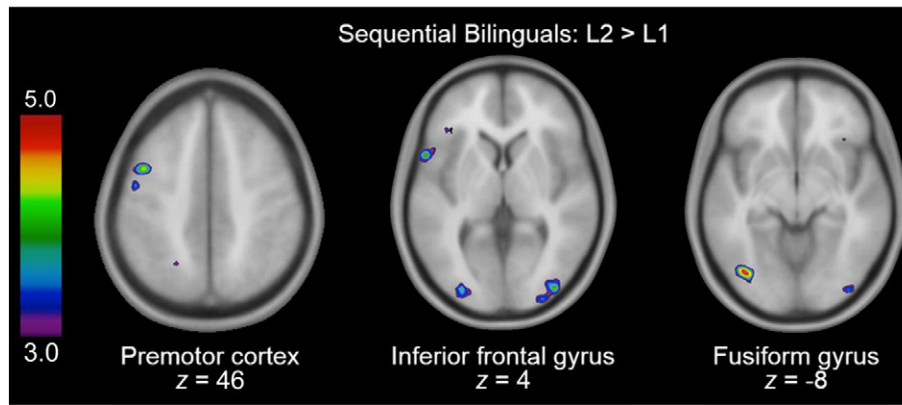
Fig. 2. Subtraction images for the direct comparison of L2 vs. L1 sentence reading in sequential bilinguals. Sequential bilinguals, when reading aloud in L2 compared to L1, activated several brain regions more significantly, including the left premotor cortex (*left*), left inferior frontal gyrus (*middle*), and left fusiform gyrus (*right*), as well as the bilateral pre-supplementary motor areas, right lateral inferior occipital cortex, and cerebellar vermis. The left hemisphere is on the left side in all horizontal sections. Threshold for *p* < .001 uncorrected significance was established at *t* = 4.3 for the voxels and *t* = 3.17 for activation clusters greater than 222 mm³ (equivalent to 28 voxels).

the brain, including the bilateral motor and auditory cortices as well as the basal ganglia and cerebellum. These areas were also activated when highly proficient sequential bilinguals read in their L2. These observations replicated findings from previous bilingual studies (Reiterer et al., 2011; Klein et al., 2006; Rüschemeyer et al., 2006; Frenck-Mestre et al., 2005).

We next evaluated whether there was a BOLD signal difference when subjects read in their native and non-native languages. A within-group, between-language subtraction analysis revealed that when simultaneous bilinguals read in either of their two natively-acquired, orthographically similar languages, they engaged the same brain regions to the same extent. However, sequential bilinguals recruited speech-motor regions including the left IFG and left premotor cortex more strongly when reading aloud in their non-native language. Here, too, our results confirm previous reports that show a greater reliance on articulatory-motor areas such as the IFG and premotor cortex when late L2 learners speak in their second language (Hu et al., 2013; Liu et al., 2010; Klein et al., 2006; Rüschemeyer et al., 2006). A regression analysis performed with age of acquisition in all bilingual subjects during English sentence reading, demonstrated a significant positive correlation between AoA and functional activation in the left premotor cortex, left inferior frontal gyrus, bilateral fusiform gyrus, right anterior cingulate cortex, and bilateral occipital cortex. These results further suggest that age of acquisition is a determining factor for the greater functional activity observed in bilinguals during speech production in a non-native language, in that the earlier in life the speaker acquires an L2, the less he appears to rely on sensorimotor and phonological processing brain areas while reading aloud.

Interestingly, sequential bilinguals' accents in L2 were judged by independent raters to be less native-like than in L1 and less native-like than the accents of simultaneous bilinguals in their two languages.

Perhaps as a result of greater difficulty in producing native-like accent in their L2, sequential bilinguals recruit the articulatory-motor areas more strongly to manage the demands of speaking a non-native language. In support of this interpretation, Rüschemeyer et al. (2006) found greater involvement of the motor cortex during non-native language reading, even when articulation in the second language was covert. There is evidence that the left premotor cortex is involved in feed-forward computations enabling accurate auditory-motor timing, a requirement for speech articulation (Kornysheva and Schubotz, 2011; Neef et al., 2011). Furthermore, Hu et al. (2013) observed that late bilinguals who were more adept at L2 pronunciation demonstrated increased activation of the left IFG and motor cortex. Like Hu et al.'s late bilingual group with advanced L2 pronunciation, our sequential bilinguals, despite having less native-like accents in L2, were nevertheless quite successful in their ability to articulate accurately. When contrasted
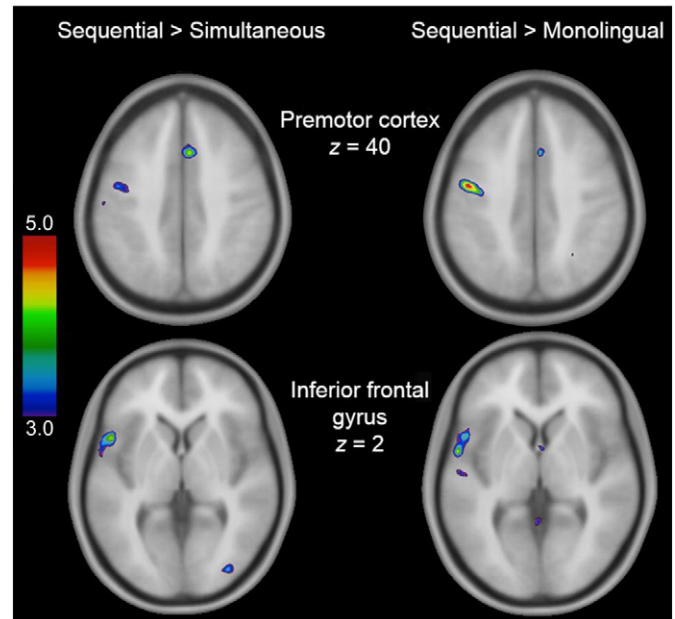
Table 6
Areas of greater activation in L2 than L1 for sequential bilinguals.

Brain area	L2 > L1		
	x, y, z	*t*	Cluster volume (mm³)
Left hemisphere			
Pre-supplementary motor area	−2, 10, 56	3.9	760
Inferior frontal gyrus	−58, 12, 4	4.0	568
Premotor cortex	−44, 6, 46	4.2	2096
Fusiform gyrus	−38, −74, −8	5.0	1016
Cerebellar vermis	−1, −73, −24	3.9	536
Right hemisphere			
Pre-supplementary motor area	2, 13, 56	3.6	760
Occipital cortex	38, −86, 0	4.3	1688

Fig. 3. Group contrasts. Sequential bilinguals activated the left premotor cortex and the left inferior frontal gyrus more significantly than simultaneous bilinguals and monolinguals during English sentence reading. English was a non-native language for the sequential bilinguals, but native for both simultaneous bilinguals and monolinguals. The left hemisphere is on the left side in all horizontal sections. Threshold for *p* < .001 uncorrected significance was established at *t* = 4.3 for the voxels and *t* = 3.17 for activation clusters greater than 222 mm³ (equivalent to 28 voxels).

Table 7
Group contrasts: coordinates of activation maxima.

Brain area	Sequential > simultaneous			Sequential > monolingual		
	x, y, z	t	Cluster volume (mm³)	x, y, z	t	Cluster volume (mm³)
Left hemisphere						
Inferior frontal gyrus	−52, 12, 4	4.0	400	−62, −10, 12	4.4	576
Inferior frontal gyrus				−52, 12, 4	3.7	752
Premotor cortex	−48, −6, 40	3.2	280	−50, −8, 46	5.0	2408
Ant. sup. temporal gyrus				−60, 2, −8	3.6	752
Thalamus				−2, −16, 14	4.2	1600
Right hemisphere						
Cingulate	6, 18, 40	3.9	288	4, 16, 38	3.8	72[a]
Thalamus	2, −6, 10	3.7	88[a]	2, −6, 10	4.8	1600
Posterior cerebellum	16, −86, −42	4.2	600	10, −76, −48	4.5	3240

[a] These peaks demonstrated a trend and were included in the table as a point of comparison between the two groups.

with the simultaneous bilinguals and monolinguals, the sequential bilinguals reading aloud in their L2 also recruited the right anterior cingulate cortex. It appears that native-like accent, known to be difficult to acquire in L2, especially in adulthood, is accompanied by increased activation for both the motor act of speaking and the monitoring of speech output.

Additional support for the notion that there is greater activation when speaking in a late-acquired L2 comes from our comparison of sequential bilinguals with the other two groups. As hypothesized, the sequential bilinguals recruited the left premotor cortex and left inferior frontal gyrus more robustly than did either monolinguals or simultaneous bilinguals during English sentence reading. Since English is a non-native language for the sequential bilinguals, but a native language for the other groups, this finding was not unexpected. This extra burden was manifested behaviorally by sequential bilinguals who took longer to read in English than did either simultaneous bilinguals or monolinguals. Also in line with our previous predictions, English-speaking monolinguals produced cortical activation patterns similar to those of simultaneous bilinguals when they read in their native language. However, when reading aloud in French, a language to which they were only passively exposed, monolinguals not only activated these cortical areas more extensively than did either bilingual group, but they also recruited additional brain structures important for articulation, such as the left frontal operculum and anterior insula. This augmented activation likely reflects the greater articulatory demand imposed by novel words with unfamiliar and unpracticed pronunciation (Simmonds et al., 2011b), expressed behaviorally by a significant increase in sentence production time.

The left fusiform gyrus of the occipitotemporal cortex also emerged as a locus more highly recruited in a non-native language for sequential bilinguals. This brain region, believed to contain the visual word form area for the recognition of the written word (Dehaene et al., 2010; McCandliss et al., 2003; Cohen et al., 2002), is involved in the orthographic-to-phonological transformation in overt reading. For the sequential bilinguals, the increased fusiform activity is a probable consequence of late L2 acquisition, in that a decreased capacity for developing native-like phonology necessitates greater activation of this region for successful decoding of the print-to-sound correspondence. Sequential bilinguals also showed greater activity in occipital cortex when reading in L2 after subtraction of the visual baseline.
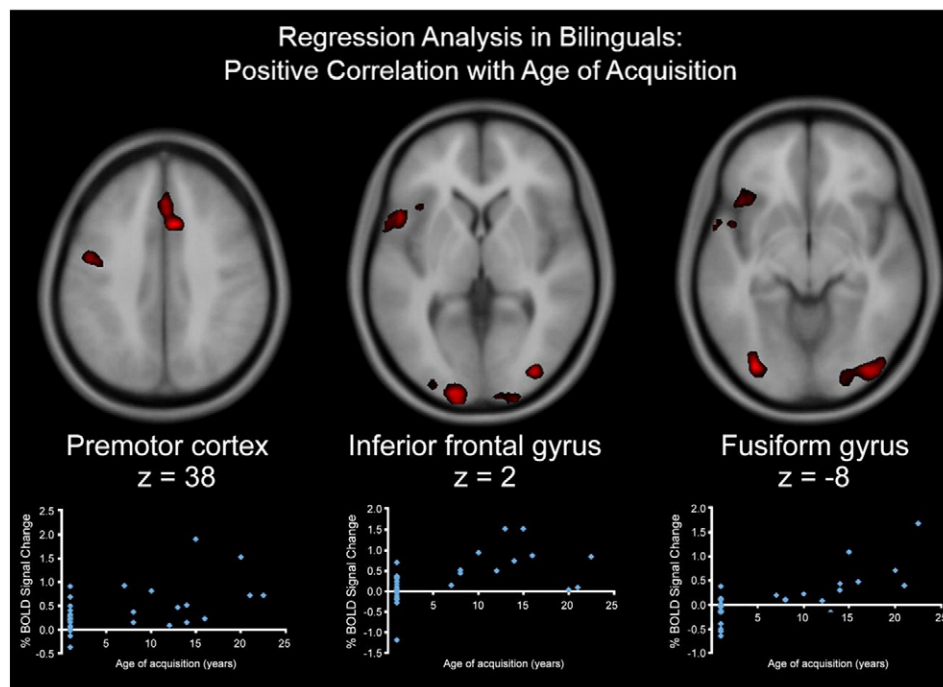

Fig. 4. Regression analysis with age of acquisition. A positive correlation between age of acquisition and functional activity during English reading was observed in the left premotor cortex (*left panel*), left inferior frontal gyrus (*middle*), and left fusiform gyrus (*right panel*). Chronological age was included in the analysis as a covariate of non-interest. The left hemisphere is on the left side in all horizontal sections.

Table 8
Regression analysis. Positive correlation with age of acquisition.

Brain area	x, y, z	r	p
Left hemisphere			
Inferior frontal gyrus	−50, 12, 2	0.591	0.004
Premotor cortex	−48, −4, 38	0.583	0.004
Fusiform gyrus	−34, −84, −8	0.778	0.001
Occipital cortex	−34, −86, 16	0.716	0.001
Right hemisphere			
Anterior cingulate cortex	8, 18, 38	0.636	0.001
Fusiform gyrus	38, −86, −8	0.603	0.001
Occipital cortex	34, −86, 8	0.572	0.006

This suggests that cortical areas involved in the basic stages of visual processing and in sustaining visual attention are impacted during reading when a language is learned late. Another explanation for these observed patterns relates to differences between the orthographic depth of English and French. However, this interpretation is unlikely since sentence stimuli were constructed to minimize print-to-sound irregularities and no language-related differences were observed in the simultaneous bilinguals who were exposed to both English and French orthography from birth.

Taken together, this investigation builds on the behavioral studies discussed earlier (Kuhl, 2010; Werker and Lalonde, 1988; Werker and Tees, 1984) to show how AoA constraints for developing native-like phonology are manifest at the neural level. When language is learned from birth, it appears that subsequent use involves the same neural substrate to a comparable degree regardless of the monolingual or bilingual status of the speaker. Language acquired later in life, however, requires greater activity to accommodate the increased phonological demands for non-native speech, even when mastered at high proficiency. Our findings, therefore, are consistent with the hypothesis that AoA plays a significant role in shaping the neural framework associated with language processing and production.

What has yet to be determined is whether the differences between simultaneous and sequential second language acquisition are related to the closing of a sensitive period or the form of learning. Learning a second language through an implicit process (exposure) compared to through more explicit instruction may also have a significant effect on the way that the brain processes language. Finally, these data suggest that speech production requires less neural effort when the language being spoken is learned in native fashion from birth. Such observations might relate to the reasons why simultaneous bilinguals are able speak with a native-like accent in their two languages, while late bilinguals often cannot, a difference shown by these and previous results (Klein et al., 2014) to have both functional and structural neural correlates. Further research will determine whether it is the early age of acquisition or the native setting that drives the functional signatures of simultaneous bilingualism.

Conflict of interest statement

The authors declare no conflict of interest.

Acknowledgments

References

Baayen, R.H., Piepenbrock, R., van Rijn, H., 1995. The CELEX Lexical Database. Release 2 [CD-ROM]. Linguistic Data Consortium. University of Pennsylvania, Philadelphia.

Baddeley, A.D., 2003. Working memory and language: an overview. J. Commun. Disord. 36, 189–208.

Bavelier, D., Corina, D., Jezzard, P., Padmanabhan, S., Clark, V.P., Karni, A., et al., 1997. Sentence reading: a functional MRI study at 4 Tesla. J. Cogn. Neurosci. 9 (5), 664–686.

Bialystok, E., 1997. The structure of age: in search of barriers to second language acquisition. Second. Lang. Res. 13, 116–137.

Birdsong, D., 1999. Introduction: whys and why nots of the critical period hypothesis for second language acquisition. In: Birdsong, D. (Ed.), Second Language Acquisition and the Critical Period Hypothesis. Erlbaum, Mahwah, N. J., pp. 161–181.

Birdsong, D., 2005. Interpreting age effects in second language acquisition. In: Kroll, J., de Groot, A. (Eds.), Handbook of Bilingualism: Psycholinguistic Perspectives. Cambridge Univ Press, New York, pp. 109–127.

Boersma, Paul, 2001. Praat, a system for doing phonetics by computer. Glot Int. 5 (9/10), 341–345.

Burns, T.C., et al., 2007. The development of phonetic representation in bilingual and monolingual infants. Appl. Psycholinguist. 28, 455–474.

Christiner, M., Reiterer, S., 2013. Song and speech: examining the link between singing talent and speech imitation ability. Front. Psychol. 4 (874). http://dx.doi.org/10.3389/fpsyg.2013.00874.

Cobb, T., 2009. The Compleat Lexical Tutor. www.lextutor.ca (Accessed 18 September 2012).

Cohen, L., Lehéricy, 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.

Collins, D.L., Neelin, P., Peters, T.M., Evans, A.C., 1994. Automatic 3D intersubject registration of MR volumetric data in standardized Talairach space. J. Comput. Assist. Tomogr. 18, 192–205.

Dehaene, S., Pegado, F., Braga, L.W., et al., 2010. How learning to read changes the cortical networks for vision and language. Science 330, 1359–1364.

Fiez, J.A., Petersen, S.E., 1998. Neuroimaging studies of word reading. PNAS 95, 914–921.

Flege, J.E., Yeni-Komshian, G.H., Liu, S., 1999. Age constraints on second-language acquisition. J. Mem. Lang. 41, 78–104.

Frenck-Mestre, C., Anton, J.L., Roth, M., Vaid, J., Viallet, F., 2005. Articulation in early and late bilinguals' two languages: evidence from functional magnetic resonance imaging. Neuroreport (7), 761–765.

Gathercole, S.E., Willis, C.S., Baddeley, A.D., Emslie, H., 1994. The children's test of non-word repetition: a test of phonological working memory. Memory 2, 103–127.

Gathercole, S.E., Hitch, G.J., Service E., Martin, A.J., 1997. Phonological short-term memory ad new word learning in children. Dev. Psychol. 33, 966–979.

Golestani, N., Zatorre, R.J., 2004. Learning new sounds of speech: reallocation of neural substrates. NeuroImage 21, 494–506.

Golestani, N., Zatorre, R.J., 2009. Individual differences in the acquisition of second language phonology. Brain Lang. 109, 55–57.

Golestani, N., Paus, T., Zatorre, R.J., 2002. Anatomical correlates of learning novel speech sounds. Neuron 35 (5), 997–1010.

Golestani, N., Molko, M., Dehaene, S., Lebihan, D., Pallier, C., 2007. Brain structure predicts the learning of foreign speech sounds. Cereb. Cortex 17, 575–582.

Goswami, U., 2008. The development of reading across languages. Ann. N. Y. Acad. Sci. 1145, 1–12.

Gracco, V.L., Tremblay, P., Pike, B., 2005. Imaging speech production using fMRI. NeuroImage 26, 294–301.

Hatzidaki, A., Branigan, H.P., Pickering, M.J., 2011. Co-activation of Syntax in Bilingual.

Hu, X., Ackermann, H., Martin, J.A., et al., 2013. Language aptitude for pronunciation in advanced second language (L2) learners: behavioral predictors and neural substrates. Brain Lang. http://dx.doi.org/10.1016/j.bandl.2012.11.006.

Indefrey, P., 2006. A meta-analysis of hemodynamic studies on first and second language processing: which suggested differences can we trust and what do they mean? Lang. Learning 56 (S1), 279–304.

Indefrey, P., 2012. Hemodynamic studies of syntactic processing. In: Faust, M. (Ed.), The Handbook of the Neuropsychology of Language. Volume 1&2. Wiley-Blackwell, Oxford, UK.

Johnson, J.S., Newport, E.L., 1989. Critical period effects in second language learning: the influence of maturational state on the acquisition of English as a second language. Cogn. Psychol. 21, 60–99.

Klein, D., Zatorre, R.J., Milner, B., Meyer, E., Evans, A.C., 1994. Left putaminal activation when speaking a second language: evidence from PET. Neuroreport 5, 2295–2297.

Klein, D., Milner, B., Zatorre, R.J., Meyer, E., Evans, A.C., 1995. The neural substrates underlying word generation: a bilingual functional imaging study. Proc. Natl. Acad. Sci. U. S. A. 92, 2899–2903.

Klein, D., Watkins, K.E., Zatorre, R.J., Milner, B., 2006. Word and nonword repetition in bilingual subjects: a PET study. Hum. Brain Mapp. 27, 153–161.

Klein, D., Mok, K., Chen, J.-K., Watkins, K.E., 2014. Age of language learning shapes brain structure: a cortical thickness study of bilingual and monolingual individuals. Brain Lang. 131, 20–24.

Kornysheva, K., Schubotz, R.I., 2011. Impairment of auditory-motor timing and compensatory reorganization after ventral premotor cortex stimulation. PLoS One 6 (6), e21421.

Kuhl, P.K., 2010. Brain mechanisms in early language acquisition. Neuron 65 (7), 713–727.

Lenneberg, E., 1967. The Biological Foundations of Language. Wiley, New York.

Liu, H., Hu, Z., Guo, T., Peng, D., 2010. Speaking words in two languages with one brain: neural overlap and dissociation. Brain Res. 1316, 75–82.

Long, M.H., 1990. The least a second language acquisition theory needs to explain. TESOL Q. 24 (4), 649–666.

Marian, V., 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.

Masterson, J., Druks, J., 1998. Description of a set of 164 nouns and 102 verbs matched for printed word frequency, familiarity and age-of-acquisition. J. Neurolinguistics 11 (4), 331–354.

McCandliss, B.D., Cohen, L., Dehaene, S., 2003. The visual word form area: expertise for reading in the fusiform gyrus. Trends Cogn. Sci. 7 (7), 293–299.

Neef, N.E., Jung, K., Rothkegel, H., Pollok, B., von Gudenberg, A.W., Sommer, M., 2011. Right-shift for non-speech motor processing in adults who stutter. Cortex 47 (8), 945–954.

Nosarti, C., Mechelli, A., Green, D.W., Price, C.J., 2010. The impact of second language learning on semantic and nonsemantic first language reading. Cereb. Cortex 20, 315–327.

Parker Jones, O., Green, D.W., Grogan, A., et al., 2012. Where, when and why brain activation differs for bilinguals and monolinguals during picture naming and reading aloud. Cereb. Cortex 22, 892–902.

Parker Jones, O., Seghier, M.L., Kawabata Duncan, K.J., et al., 2013. Auditory-motor interactions for the production of native and non-native speech. J. Neurosci. 33 (6), 2376–2387.

Perani, D., Paulesu, E., Galles, N.S., Dupoux, E., Dehaine, S., Bettinardi, V., Cappa, S.F., Fazio, F., Mehler, J., 1998. The bilingual brain. Proficiency and age of acquisition of the second language. Brain 121 (10), 1841–1852.

Price, C.J., 2010. The Anatomy of Language: A Review of 100 fMRI Studies Published in 2009. The Year in Cog. Neurosci 1191 pp. 62–88.

Price, C.J., 2012. A review and synthesis of the first 20 years of PET and fMRI studies o heard speech, spoken language and reading. NeuroImage 62 (2), 816–847.

Reiterer, S.M., Hu, X., Erb, M., et al., 2011. Individual differences in audio-vocal speech imitation in late bilinguals: functional neuro-imaging and brain morphology. Front. Psychol. 2, 271.

Rüschemeyer, S.-A., Zysset, S., Friederici, A.D., 2006. Native and non-native reading of sentences: an fMRI experiment. NeuroImage 31 (1), 354–365.

Simmonds, A.J., Wise, R.J.S., Dhanjal, N.S., Leech, R., 2011a. A comparison of sensory-motor activity during speech in first and second languages. J. Neuropsychol. 106, 470–478.

Simmonds, A.J., Wise, R.J.S., Leech, R., 2011b. Two tongues, one brain: imaging bilingual speech production. Front. Psychol. 2 (166), 1–13.

Talairach, J., Tournoux, P., 1988. Co-planar Stereotaxic Atlas of the Human Brain. Thieme Medical, New York.

Tan, L.H., Spinks, J.A., Feng, C.-M., et al., 2003. Neural systems of second language reading are shaped by native language. Hum. Brain Mapp. 18, 158–166.

Thorn, A.S.C., Gathercole, S.E., 2001. Language differences in verbal short-term memory do not exclusively originate in the process of subvocal rehearsal. Psychon. Bull. Rev. 8, 357–364.

Wartenburger, I., Heekeren, H.R., Abutalebi, J., Cappa, S.F., Villringer, A., Perani, D., 2003. Early setting of grammatical processing in the bilingual brain. Neuron 37 (1), 159–170.

Wechsler, D., 1981. Manual for the Wechsler Adult Intelligence Scale—Revised. The Psychological Corporation, San Antonio, TX.

Werker, J.F., Byers-Heinlein, K., 2008. Bilingualism in infancy: first steps in perception and comprehension. Trends Cogn. Sci. 12 (4), 144–151.

Werker, J.F., Lalonde, C.E., 1988. Cross-language speech perception: initial capabilities and developmental change. Dev. Psychol. 24, 672–683.

Werker, J.F., Tees, R.C., 1984. Phonemic and phonetic factors in adult cross-language speech perception. J. Acoust. Soc. Am. 75 (6), 1866–1878.

Worsley, K.J., Liao, C., Aston, J., Petre, V., Duncan, G.H., Morales, F., Evans, A.C., 2002. A general statistical analysis for fMRI data. NeuroImage 15 (1), 15.

Ziegler, J.C., Goswami, U., 2005. Reading acquisition, developmental dyslexia, and skilled reading across languages: a psycholinguistic grain size theory. Psychol. Bull. 131 (1), 3–29.