

Bilingual brain organization: A functional magnetic resonance adaptation study

Denise Klein,* Robert J. Zatorre, Jen-Kai Chen, Brenda Milner, Joelle Crane, Pascal Belin, and Marc Bouffard

Cognitive Neuroscience Unit, Montreal Neurological Institute, 3801 University Street, Montreal, Quebec, Canada H3A 2B4

Received 13 May 2005; revised 17 November 2005; accepted 7 December 2005
Available online 3 February 2006

We used functional magnetic resonance adaptation (fMRA) to examine whether intra-voxel functional specificity may be present for first (L1)- and second (L2)-language processing. We examined within- and across-language adaptation for spoken words in English–French bilinguals who had acquired their L2 after the age of 4 years. Subjects listened to words presented binaurally through earphones. In two control conditions (one for each language), six identical words were presented to obtain maximal adaptation. The remaining six conditions each consisted of five words that were identical followed by a sixth word that differed. There were thus a total of eight experimental conditions: no-change (sixth word identical to first five); a change in meaning (different final word in L1); a change in language (final item translated into L2); a change in meaning and language (different final word in L2). The same four conditions were presented in L2. The study also included a silent baseline. At the neural level, within- and across-language word changes resulted in release from adaptation. This was true for separate analyses of L1 and L2. We saw no evidence for greater recovery from adaptation in across-language relative to within-language conditions. While many brain regions were common to L1 and L2, we did observe differences in adaptation for forward translation (L1 to L2) as compared to backward translation (L2 to L1). The results support the idea that, at the lexical level, the neural substrates for L1 and L2 in bilinguals are shared, but with some populations of neurons within these shared regions showing language-specific responses.

© 2005 Elsevier Inc. All rights reserved.

Keywords: Adaptation; fMRI; Neuroimaging; Repetition suppression; Speech perception; Language; Frontal lobes; Semantic priming

Introduction

A central issue in understanding how experience with language may influence wiring in the brain is whether there are critical periods for the development of language and whether the neural substrates

involved in processing a second language (L2) are the same as those of a native language (L1). This question was originally posed by Pitres (1895) after observing the variable recovery patterns of the different languages of polyglot aphasic patients (Paradis, 1989, 1997), but, to date, “no correlation has been found between pattern of recovery and neurological, etiological, experiential or linguistic parameters: not site, size or origin of lesion, type or severity of aphasia, type of bilingualism, language structure or factors related to acquisition or habitual use” (Paradis, 1995, p. 211).

Neuroimaging methods have recently been employed to explore the issue because, unlike lesion studies, which depend on experiments of nature, a particular advantage of functional neuroimaging is the possibility to conduct controlled experiments. Despite this advantage, the brain imaging studies on the cortical representation of L2 are not unequivocal. In earlier PET studies, we examined whether common cortical substrates are involved when bilingual speakers conduct searches within and across languages. We observed the same patterns of activation across languages and across tasks (Klein et al., 1994, 1995, 1999). The results from several PET and fMRI studies support this claim for similar patterns of cerebral representation across languages in bilingual individuals (Perani et al., 1996; Chee et al., 1999a,b; Price et al., 1999; Illes et al., 1999; Hernandez et al., 2000). However, several authors have proposed that the patterns of representation for the L1 and L2 may vary within the language-dominant hemisphere of a bilingual subject, with factors such as age of acquisition of the L2 (e.g., Kim et al., 1997; Dehaene et al., 1997) and proficiency in each language (Perani et al., 1998) being responsible for the differing patterns. Two important factors in the debate are the resolving power of the techniques used and the methods of data analysis. To date, the contrasting claims could not be well evaluated because conventional brain-mapping methods that measure the overall neural activation within a voxel may average out a heterogeneous group of highly selective neurons, making it difficult to assess from the measured fMRI signal whether its source is the activity of a mixture of neuronal populations, each tuned to a different property, or whether it is the outcome of the activity of a homogeneous group of neurons that share a common

* Corresponding author. Fax: +1 514 398 1338.

E-mail address: denise.klein@mcgill.ca (D. Klein).

Available online on ScienceDirect (www.sciencedirect.com).

property (Grill-Spector and Malach, 2001). Recent studies have sought to overcome the problem of spatial averaging by using functional magnetic resonance adaptation (fMRA), which makes use of the property some neurons display of reducing their response to a sensory stimulus that is repeatedly presented (Grill-Spector et al., 1999).

Owing to the fact that fMRA enables one to tag specific neuronal populations within an area and investigate their functional properties (Grill-Spector et al., 1999; Grill-Spector and Malach, 2001), it seems to be an appropriate tool for studying the differences between L1 and L2 processing. In the present experiment, we examined the specific populations of neurons active in L1 and L2, using an fMR adaptation technique in order to distinguish whether voxels in a particular area contain neuronal populations each tuned to a different language or whether these neurons are language-insensitive.

In word recognition, sensory input from a word is assumed to activate the mental representation corresponding to that word. Since a certain amount of the activation outlasts the stimulus duration, lexical access for the same word is facilitated on second presentation (Schacter and Buckner, 1998). At the neural level, repetition can lead to decreased activation in brain regions that were activated during the initial processing of a stimulus (Schacter and Buckner, 1998; Wiggs and Martin, 1998; Wagner et al., 2000). Such a “repetition suppression” response is a reduction in brain activity with repeated stimulus presentation (Desimone, 1996) and is similar to fMRA. Using fMRA, we can compare the activation elicited by identical words to that elicited by words with the same meaning in a different language (translation) or by different words in either the L1 or the L2. Presenting a word in L1 repetitively will lead to the suppression of the activation of the neurons within the voxel that are tuned to L1, resulting in a reduced fMR signal. If the neurons within the voxel are truly language-insensitive, then introducing the L2 will produce continuing adaptation, similar to that produced by the L1, since the neurons will be essentially “blind” to this manipulation. If, on the other hand, the voxels contain a mixture of neuronal groups, each tuned to a different language, then each language should activate a new group of neurons, the L2 neurons would not be adapted, and the result will be a strong fMRI signal, i.e., recovery from the adapted state (Grill-Spector et al., 1999).

Chee et al. (2003) recently evaluated adaptation effects in fluent English–Chinese bilinguals using fMRA and a visual reading task. Using English only and mixed Chinese–English conditions, they were able to conclude that, in English–Chinese early bilinguals who were proficient in their two languages, semantic representations for English and Chinese concrete nouns share neuronal networks. Chee et al.’s (2003) findings suggested that fMRA revealed neuronal networks that discriminate word semantics but not language. Cortical substrates involved in such a ‘shared semantic network’ were located in the left prefrontal and temporal areas of the brain. Chee et al. (2003) suggested that there also exists a language-dependent neural network because a mixed-language condition showed greater signal change than an English-only condition in the left prefrontal and in lateral and inferior temporal regions. They interpreted this increase in signal change as reflecting the greater attentional resources needed when reading different scripts in the two languages.

The current experiment differs from that of Chee et al. (2003) in that we evaluated adaptation effects in the auditory modality in English–French subjects, so as to tap primary language processes. We also made use of a balanced design enabling us to look at the L1 and L2 independently, to examine translation direction, from L1

into L2 and from L2 into L1 (“forward” and “backward” translation, respectively), and to investigate semantic change in both the L1 and L2.

In our early brain imaging studies (Klein et al., 1995), translation of single words by English–French bilinguals elicited activation increases mainly in the left inferior frontal and dorsolateral prefrontal cortices. Rinne et al.’s (2000) findings using PET in professional interpreters during simultaneous interpreting also emphasized the importance of the left inferior frontal and dorsolateral frontal cortex in translation performance. Studies using tasks where translation and strategic manipulation are required, as when subjects name pictures and are asked to switch between languages, have also activated the dorsolateral prefrontal cortex (Hernandez et al., 2001). Price et al. (1999) failed to replicate these findings, however, in a PET activation study employing a similar word-level translation task (German–English). Price et al. (1999) suggest that active translation and switching may be mediated by partially independent mechanisms. They observed that switching the input language resulted in activation of Broca’s area and the supramarginal gyri, areas associated with phonological recoding. The discrepancies between studies may be related to differences in the task requirements, the nature of the baseline task and differences in language proficiency of the participants.

Although, in our original study, we did not see different patterns of activation related to direction of translation, Rinne et al. (2000) showed that brain activation patterns were clearly modulated by direction of translation, with more extensive activation during translation into the non-native language. Price et al. (1999) suggest that, in forward translation (i.e., L1 → L2), the semantic route dominates, whereas, in backward translation (i.e., L2 → L1), the lexical route dominates, reflecting the acquisition of the L2 word in the context of a pre-existing lexical concept–word form link in L1. In behavioral studies, Kroll and Stewart (1994) have shown that directionality effects occur when using translation tasks; translating words from L1 to L2 (forward) takes longer than translating from L2 to L1 (backward), and they have argued that forward translation proceeds via conceptual memory, whereas backward translation typically exploits the direct links between nodes in lexical memory. This asymmetry effect has been observed both for relatively proficient and for less proficient bilingual subjects, although it is larger for the latter group of subjects (Kroll and Stewart, 1994).

The goal of the present study was to determine whether overlap exists in the brain regions responsible for processing heard words in L1 and L2, as demonstrated by fMR adaptation. If a word and its translation share a common representational system and share the same underlying neural representations, then cross-language adaptation should be observed. However, if a bilingual’s two languages are stored in separate language-specific lexicons with populations of neurons that are language-sensitive, then no cross-language adaptation should be observed.

Methods

Subjects

The participants were 16 bilingual adults, with English as their native language (L1) and who spoke French as a second language (L2). They were students recruited from the McGill University community in Montreal who had learned their L2 between 4 and 12 years of age. These subjects were recruited after having

completed a language-background questionnaire with measures of current fluency in the L2, and they ranged in proficiency from highly proficient to low-proficiency bilinguals. Table 1 shows proficiency scores and age of acquisition for each subject. The subjects gave informed consent, and the study was approved by the Research Ethics Board of the Montreal Neurological Institute.

Procedure

The experiment comprised of eight conditions (4 in L1 and 4 in L2) plus a silent baseline condition. There were two conditions, one for each language, where six words were presented with no items varied to obtain maximal adaptation (\emptyset^1 = no-change L1; \emptyset^2 = no-change L2). In the remaining six conditions, each condition consisted of six words; the first five of these were identical, but the last word was varied (see Table 2). These conditions consisted of (1) a change in meaning (ΔM^1 ; the same word presented with a final word in L1 varied); (2) a change in language (ΔL^1 = same word presented with the final item a translation from L1 to L2); (3) a change in language and meaning (ΔLM^1 = same word in L1 with final word in L2 semantically unrelated). The same conditions were presented in the L2 (ΔM^2 , ΔL^2 , ΔLM^2). Lists were matched across languages, so that stimuli were equated on a range of psycholinguistic variables (word frequency, imageability and syllable number). All stimuli were equated for RMS amplitude using Mitsyn (WLH, MA, USA).

Scanning

The scans were acquired on a 1.5 T Siemens Vision imager. A high-resolution T1-weighted 3D volume was acquired for anatomical localization (matrix size $256 \times 256 \times 170$, voxel size $1 \times 1 \times 1 \text{ mm}^3$) followed by echo-planar imaging (EPI). Functional images were acquired in a plane parallel to the

Table 1
Proficiency ratings and age of acquisition (AoA) of L2

Subject no.	#Syllables L2/L1	PPVT (%)	Proficiency	AoA
1	82	58	140	6
2	73	77	150	6
3	35	72	107	10
4	67	73	140	12
5	89	75	164	5.5
6	65	67	132	12
7	92	68	160	6
8	65	70	135	5.5
9	110	67	177	14
10	58	50	108	5.6
11	55	60	115	5.8
12	36	65	101	6
13	32	77	109	8
14	74	65	139	5.2
15	73	68	141	5.5
16	94	57	151	13

The second column displays the number of syllables produced in the picture and day descriptions in L2 relative to L1 (#syllables L2/L1), calculated as a ratio of each excerpt divided by number of syllables produced for each language. The third column (PPVT; Peabody Picture Vocabulary French version) shows the percentage correct; the fourth column (Proficiency) represents the overall proficiency score for each subject, calculated by combining the PPVT percentages correct and the #syllables L2/L1. The last column presents the age of acquisition (AoA) for each participant.

Table 2
Conditions for experiment

Block	Task	Stimulation					Target stimulus
1	L1 same word	Bed	Bed	Bed	Bed	Bed	Bed
2	L1 different word	Bed	Bed	Bed	Bed	Bed	Pig
3	L1–L2 translate	Bed	Bed	Bed	Bed	Bed	Lit
4	L1–L2 unrelated	Bed	Bed	Bed	Bed	Bed	Pomme
5	L2 same word	Lampe	Lampe	Lampe	Lampe	Lampe	Lampe
6	L2 different word	Lampe	Lampe	Lampe	Lampe	Lampe	Gant
7	L2–L1 translate	Lampe	Lampe	Lampe	Lampe	Lampe	Light
8	L2–L1 unrelated	Lampe	Lampe	Lampe	Lampe	Lampe	Grass

anterior–posterior commissural plane, with 20 slices positioned for maximum coverage of frontal, temporal and parietal lobes. Subjects lay in the scanner with eyes closed and passively listened to words presented binaurally through pneumatic earphones using Media Control Function software (Digivox, Montreal).

Within each of the two runs, subjects heard each condition 14 times ($n = 128$ volumes of acquisition). Every eighth brain volume acquired during the conditions was separated by one brain volume acquired after 12 s of silence (see Fig. 1). Each trial used different stimuli, and the conditions were pseudorandomly intermixed. The functional images were acquired with the following characteristics: gradient echo, TE = 50 ms, TR = 12 s, head coil, matrix size: 64×64 , voxel size: $5 \times 5 \times 5 \text{ mm}^3$. We applied a long TR to attenuate possible masking effects by the scanner noise (Belin et al., 1999; Hall et al., 1999) and temporal jitter to obtain optimal BOLD signal response. The final word was presented 2000–4500 ms from the time of the last acquisition.

Data analysis

BOLD signal images were smoothed (6-mm gaussian kernel), corrected for motion artefact and transformed into standard stereotaxic space (Talairach and Tournoux, 1988) using in-house software (Collins et al., 1994). A voxel-wise statistical analysis was then performed on the motion-corrected data, based on a linear model with correlated errors using fmristat (Worsley et al., 2000). For each individual, statistical maps of each of the eight experimental conditions against the silent baseline were constructed by averaging functional data across scans using linear regression analyses (Worsley et al., 2002). Finally, group-average statistical images were obtained by computing an omnibus test on individual t maps, using a pooled estimate of standard deviation (Worsley et al., 1992), and a threshold was established at $t = 4.14$ for the activation peaks or $t = 3.10$ for activation clusters greater than 222 mm^3 , based on the number of resolution elements in the acquisition volume (2880 resels). For each individual's data, regions of interest (ROIs) were defined as an 8 mm^3 sphere around the coordinates of significant peaks of activity found for any of the conditions relative to the silent baseline. Twenty-six regions of interest were examined (see Table 3); 18 ROIs were in the left hemisphere (6 frontal, 3 central, 9 temporal), and 8 were in the right hemisphere (2 central, 5 temporal and 1 parietal). The ROIs were defined using the most consistent peaks across all eight

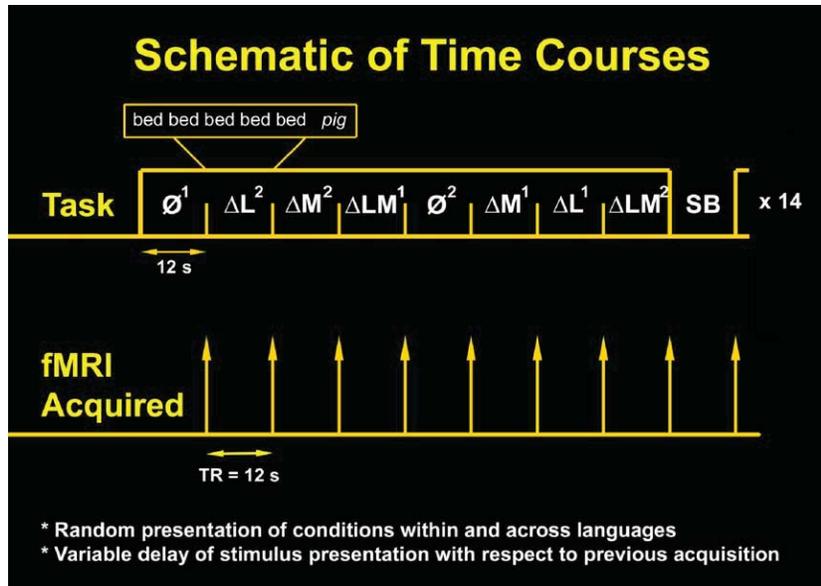


Fig. 1. Schematic representation of experiment outline. Conditions were randomly presented within and across languages. There was also a variable delay of stimulus presentation with respect to the previous acquisition. Images were acquired after the final word was presented (\emptyset = target word not changed; Δ = target word changed; M = meaning; L = language; 1 = L1; 2 = L2).

subtractions. Repeated-measures ANOVA, using the Greenhouse–Geisser conservative degrees of freedom, were performed on the percent signal change data in each region with condition as the within-subject variable. Significant effects of condition were examined further with pairwise comparisons, using the method of least significant difference.

Results

No change compared to a silent baseline

Exploratory analyses aimed at determining the brain regions activated during each experimental condition against a silent baseline revealed similar topographical patterns of activation across the conditions (Fig. 2). Table 3 lists the peaks with their location in stereotaxic coordinates and the respective brain areas. Visual inspection of the t maps in Fig. 2 indicates a clearly weaker activation for the no-change condition (i.e., \emptyset condition in both the L1 and in the L2) relative to the change conditions, especially in the left prefrontal regions. Quantitative analyses of the percentage BOLD signal changes in the ROIs confirmed this observation in 7 peaks in the left hemisphere: 3 in the inferior frontal gyrus (IFG) and 4 in the superior temporal gyrus (STG) and 3 peaks in the right hemisphere (STG) (Figs. 3 and 4). These results are consistent with our expectation of greatest habituation effects in the no-change conditions.

Word change compared to no change

Statistical analyses using fmristat (Worsley et al., 2002) were carried out to examine the effect of a change in meaning contrasted with no-word change ($\Delta M - \emptyset$), a change in language contrasted with no-word change ($\Delta L - \emptyset$) and a change in language and meaning compared with no-word change ($\Delta LM - \emptyset$). The analyses were done separately for the L1 and L2 tasks.

$\Delta M - \emptyset$

Within-language word changes (changes in word meaning in the same language) compared with no-word change caused an

Table 3

Activation peaks obtained in all 8 experimental conditions relative to silent baseline

	Stereotaxic coordinate			Anatomical location
	x	y	z	
<i>Left hemisphere</i>				
ROI 1	-48	38	6	Middle frontal gyrus (BA 46)
ROI 2	-36	20	24	Inferior frontal gyrus (BA 44)
ROI 3	-50	14	30	Inferior frontal gyrus (BA 44)
ROI 4	-48	12	24	Inferior frontal gyrus (BA 44)
ROI 5	-42	10	24	Inferior frontal gyrus (BA 44)
ROI 6	-38	10	30	Inferior frontal gyrus (BA 44)
ROI 7	-44	-4	52	Precentral gyrus (BA 4)
ROI 8	-40	-26	52	Postcentral gyrus (BA 1)
ROI 9	-38	-34	56	Postcentral gyrus (BA 1, 2)
ROI 10	-54	-2	-4	Superior temporal gyrus (BA 22)
ROI 11	-62	-2	0	Superior temporal gyrus (BA 22)
ROI 12	-54	-18	8	Superior temporal gyrus (BA 22)
ROI 13	-50	-22	6	Superior temporal gyrus (BA 22)
ROI 14	-38	-30	16	Superior temporal gyrus (BA 22)
ROI 15	-64	-36	16	Superior temporal gyrus (BA 22)
ROI 16	-50	-38	18	Superior temporal gyrus (BA 22)
ROI 17	-44	-50	-16	Inferior temporal gyrus (BA 37)
ROI 18	-30	-50	52	Superior parietal lobule (BA 7)
<i>Right hemisphere</i>				
ROI 19	54	-10	46	Precentral gyrus (BA 4)
ROI 20	38	-28	56	Postcentral gyrus (BA 1, 2)
ROI 21	52	-2	-2	Superior temporal gyrus (BA 22)
ROI 22	62	-18	6	Superior temporal gyrus (BA 22)
ROI 23	46	-22	10	Superior temporal gyrus (BA 22)
ROI 24	44	-30	10	Superior temporal gyrus (BA 22)
ROI 25	68	-30	8	Superior temporal gyrus (BA 22)
ROI 26	32	-48	56	Superior parietal (BA 7)

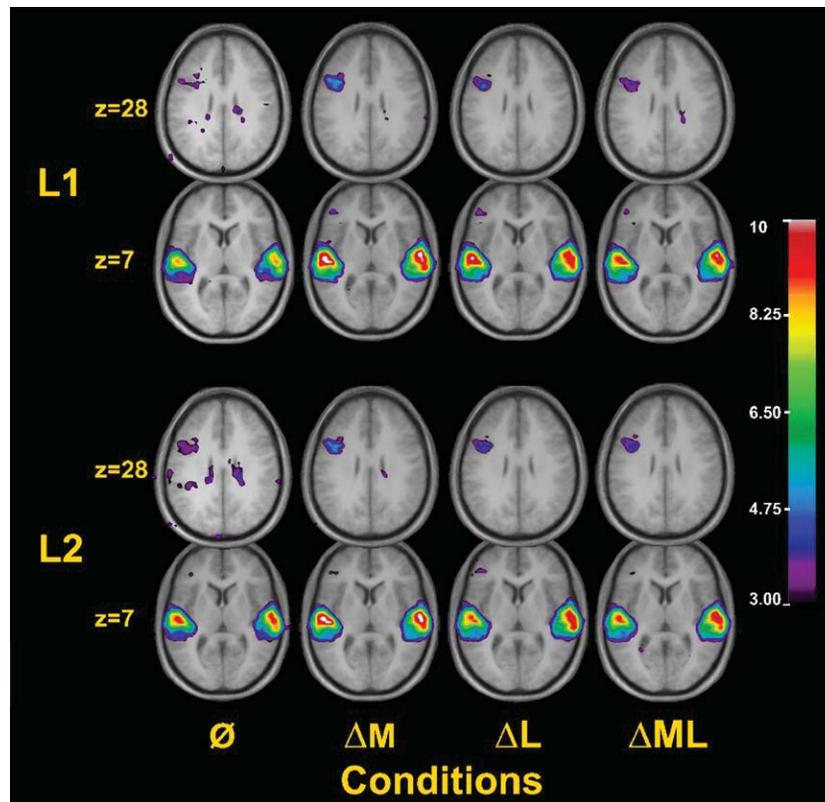


Fig. 2. Activation patterns of experimental conditions compared with the silent baseline. Left hemisphere is on the left side in all horizontal sections.

increase in fMRI signal in the left and right lateral superior temporal gyri and in the posterior left inferior frontal region (corresponding with BA 44/6). The pattern was the same for both languages (Fig. 5).

$\Delta L - \emptyset$

Whole-brain analyses for a change in language, but not meaning (i.e., a translation), resulted in a similar pattern of activity to the $\Delta M - \emptyset$ when the translation direction was forward from L1 into L2, but a different pattern was observed for backward translation from L2 into L1. For the forward translation condition, activity was observed bilaterally along the superior temporal gyrus, and unilateral peaks were evident in the left inferior frontal gyrus (BA 44/6). For the backward translation condition (L2 into L1), activity was observed bilaterally in the superior temporal region, but no activity was observed in the left inferior frontal region. In the ROI analyses, it was evident that the ventral peak (ROI 5) and the more dorsal (ROI 6) were activated in response to a change in language from L1 to L2, but not from L2 to L1. In addition to these frontal peaks, three peaks along the LSTG (ROIs 10, 12 and 16) were not responsive to a language change from L2 to L1.

$\Delta LM - \emptyset$

A change in both language and meaning revealed the same pattern as $\Delta M - \emptyset$, with increases being evident in the left and right lateral superior temporal gyri and in the left inferior frontal region (corresponding with BA 44/6). The pattern was observed

for both a change into L1 and into L2, although the frontal peak activated for the change from L2 into L1 was slightly less significant (Fig. 3) and slightly more posterior than the peaks observed in the other conditions.

Within- and across-language change

$\Delta LM - \Delta M$

Examination of a change in meaning and language (ΔML), as compared with a change in meaning but not language (ΔM), targeted regions that may be sensitive to language change. In this analysis, we examined whether the within-language change was any different from the between-language change. For both L1 and L2, no differences were observed.

$\Delta LM - \Delta L$

Examination of a change in meaning and language (ΔML), as compared with a change in language but not meaning (ΔL), targeted regions that may be sensitive to meaning. In the L1, the only region of significant activity was in the left superior temporal gyrus (BA21). In the L2, no differences were observed.

L2 vs. L1

Comparisons of L1 and L2 were done for all conditions. In the whole-brain analyses, the only comparison to reveal significant differences was in a comparison of $\emptyset^2 - \emptyset^1$ where significant activity was observed bilaterally along the superior

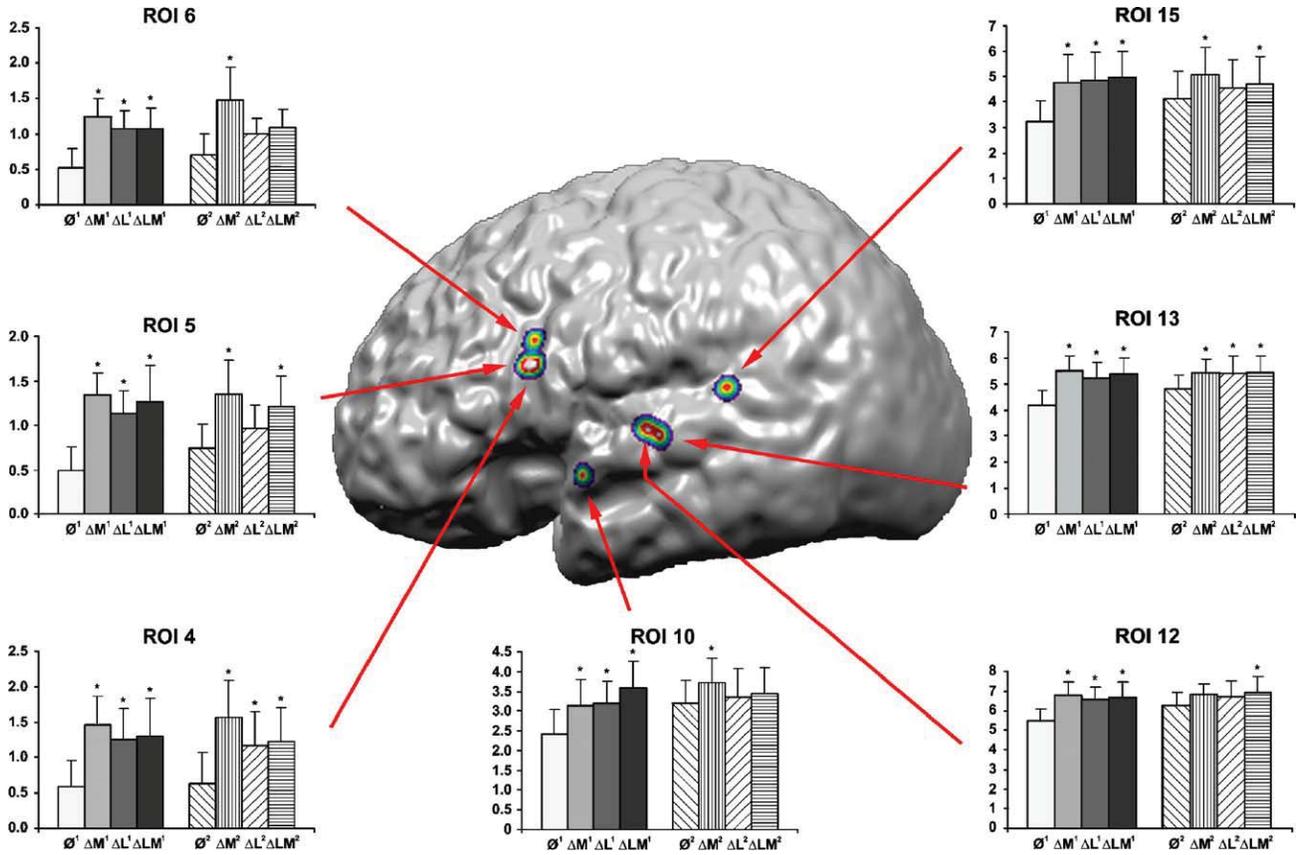


Fig. 3. Percent signal change relative to silence in the ROIs in left hemisphere (*significantly greater BOLD increase than the Ø condition within the same language $P < 0.05$).

temporal gyrus for the L2 relative to the L1. For the ROI analyses, all the ROIs along the LSTG, adapted significantly more in the L1 than the L2 (ROI 10, $P < 0.02$; ROI 11, $P < 0.01$;

ROI 12, $P < 0.04$; ROI 13, $P < 0.04$; ROI 15, $P < 0.04$), while no differences between L1 and L2 were observed for the ROIs in the RSTG.

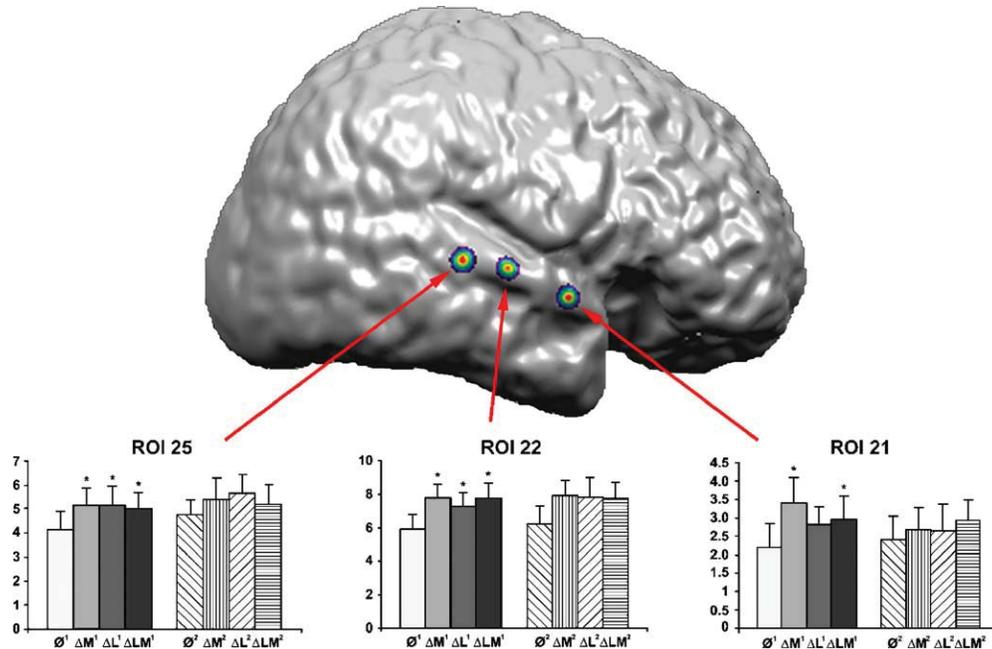


Fig. 4. Percent signal change relative to silence in the ROIs in right hemisphere (*significantly greater BOLD increase than the Ø condition within the same language, $P < 0.05$).

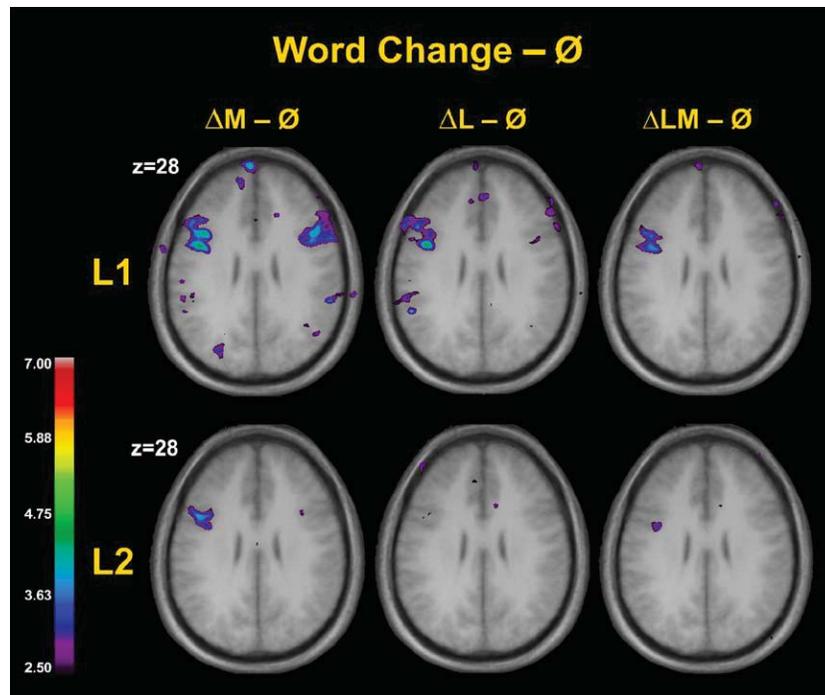


Fig. 5. Areas showing greater prefrontal activity when word change conditions (meaning, language or both) were compared to no-change condition.

Proficiency and age of acquisition

Age of acquisition was not significantly correlated with any of the conditions. The only condition that showed a correlation with proficiency was the contrast of backward translation from L2 into L1 (ΔL^2). As measured by a combined score of picture vocabulary and verbal fluency (see Table 1), a significant negative correlation was observed between the proficiency score and BOLD signal in ROI 6, suggesting a decrease in BOLD signal in the dorsal peak in the left inferior frontal gyrus with increasing proficiency ($r = -0.535$, $P < 0.05$).

Discussion

We explored whether intra-voxel functional specificity is present for first (L1)- and second (L2)-language processing by means of the functional magnetic resonance adaptation (fMRA) approach (Grill-Spector et al., 1999). In the present study, we observed decreased activity in the no-change condition, which we attribute to habituation of the signal, consistent with studies that have demonstrated habituation phenomena in response to repetition of a stimulus (Schacter and Badgaiyan, 2001). In order to explore the temporal dynamics of these processes, we have subsequently examined ERP measures of within- and across-language priming (Phillips et al., 2004). By examining the time course of habituation and priming processes in the L1 and L2, we have now obtained confirmation of the adaptation effect, in that, for both L1 and L2, the first presentation of a word in a sequence elicited a large N400 response, which then showed marked attenuation when the word was repeated in sequence three times or more (Phillips et al., 2004). The findings suggest that neural priming, as indicated by a decreased hemodynamic response, can be invoked without requir-

ing explicit or intentional retrieval of semantic information since in these experiments the subjects listened passively to the words.

Both within-language and across-language word changes compared with the no-word change condition resulted in increased BOLD signal changes. This was true for separate analyses of L1 and L2 tasks. We saw no evidence for greater recovery from adaptation (increases in fMRI signal) in across-language conditions relative to within-language conditions. While there was strong overlap in the brain regions activated for L1 and L2, we did observe some differences in BOLD response patterns for the L1 and L2. In the L1, a word change, irrespective of condition or language, resulted in extensive bilateral activations of the primary and secondary auditory areas, in regions similar to what has been previously reported (e.g., Wise et al., 1991). In addition to increased activation in modality-specific brain regions involved in the initial perception of the stimuli, regions in the posterior left inferior frontal gyrus at or near Brodmann's area 44/6 were activated. The findings implicate the posterior left inferior frontal gyrus in passive listening to a word change and the automatic semantic processing that this entails and provide support for the proposal that the LIFG is involved in accessing lexical information (e.g., Klein et al., 1995; Demb et al., 1995; Fiez, 1997; Wagner et al., 2001; Devlin et al., 2003). The present results are similar to the findings of others who have noted that the left inferior frontal region and bilateral temporal areas are components of the neuronal network that processes lexical-semantic information and are modulated by semantic priming (e.g., Kotz et al., 2002).

In the L2, changes in meaning and changes in both language and meaning resulted in increased activity bilaterally along the superior temporal gyrus and in the left inferior frontal region, but changes in language alone did not yield the expected activation in the LIFG. The observed asymmetrical priming in L1 and L2 indicates that semantics played a somewhat more important role in

forward than in backward translation, in keeping with what is observed in behavioral experiments (e.g., de Groot et al., 1994). Our findings suggest that either access to the L2 word automatically activated the L1 equivalent so that, when subjects heard “lit lit lit lit”, they automatically thought of the English word “bed” or possibly that subjects were consciously translating in this condition. Moreover, in this L2–L1 translation condition, increased proficiency correlated with a decrease in BOLD signal activation in the dorsal left inferior frontal region. Several cognitive studies indicate that the organization of the second language changes during the acquisition process. For example, in early stages of learning, L2 vocabulary items are processed primarily through association with their translation equivalents in the L1, whereas, in later stages of learning, they are more directly associated with their meanings (Chen and Leung, 1989; Potter et al., 1984). In this study, L1 and L2 vocabulary appear to access a common semantic system as a person becomes proficient in L2, so that a direct translation results in a decrease in signal, implying less release from adaptation in more proficient bilinguals. These findings are in keeping with those of Wartenburger et al. (2003) who used fMRI to investigate the effects of age of acquisition and proficiency level on neural correlates of grammatical and semantic judgments in Italian–German bilinguals who had learned the L2 at different ages and had different proficiency levels. They found that, while the pattern of brain activity for semantic judgments was largely dependent on proficiency level, age of acquisition mainly affected the cortical representation of grammatical processing.

Our finding that a word switch activates a dorsal region of the left posterior inferior frontal cortex is similar to the finding of Price et al. (1999). These authors suggested that switching modulates word processing at a phonological stage, a suggestion not dissimilar to that of Rodriguez-Fornells et al. (2002), who propose that bilinguals use an indirect phonological route to access the lexicon to avoid interference. This region of the dorsal left posterior inferior frontal cortex activated in our study has often been associated with phonological processing because it has been shown to be most active on tasks requiring phonemic detection (Zatorre et al., 1996; Burton et al., 2000).

It is also of interest to note that, although activation is observed bilaterally along the superior temporal gyrus, the temporal peaks extend more posteriorly in the left hemisphere. In the superior temporal region (see Figs. 3 and 4, and also Table 3), ROI 15 is 8 mm more posterior in the left hemisphere relative to ROI 25 in the right hemisphere, underlining the role of this more posterior region in language processing, a region that has also been linked to phonological processing (see Demonet et al., 1992; Zatorre et al., 1992; Callan et al., 2004; Scott and Johnsrude, 2003).

Within the left superior temporal gyrus, we observed significantly lower fMRI signal in L1 than in L2, and this was the only brain region to show this difference. These results are consistent with an ERP study in which we used a similar paradigm and obtained similar findings (Phillips et al., 2004). The decreased BOLD response in this area is in keeping with the evidence from lesion, ERP and neuroimaging studies that show that the left temporal region plays a significant role in semantic memory and comprehension (Binder et al., 1997; Damasio and Damasio, 1992; de Zubicaray et al., 2001; Hart and Gordon, 1990; Nobre and McCarthy, 1995; Vandenberghe et al., 1996). Our results support the argument that the reduced neural activity associated with repetition priming reflects more efficient or faster processing due to lowered thresholds for activating existing representations (Henson

et al., 2000). In accordance with recent neuroimaging accounts of repetition priming, it is argued that the reductions in the BOLD response reflect the decreased neural activity required for recognizing targets, even more so for L1 than L2, as these words are easier to process owing to lowered recognition thresholds via spreading activation (Schacter and Buckner, 1998; Stowe et al., 1999). It is important to note, however, that in the present study the data have been combined across subjects, allowing for maximum sensitivity and generality, but future studies with analysis of individual data using intrasubject averaging would also be important for clarification of the group findings. For example, knowledge of the individual contributions to the group mean and of how individual levels of proficiency and exposure to L2 affect the hemodynamic response might shed light on the differences observed between L1 and L2.

In keeping with Chee et al.’s (2001) findings, we failed to observe greater increases in fMRI signal related to language change than to word change; however, we did observe that, in both the left frontal and temporal regions, there were some instances where the responses to habituation in each language appeared to be mediated by distinct neural systems. The results support the notion that the mental representation of words in a bilingual’s two languages are integrated within a shared representational system, but we propose that different neuronal populations exist for the perception of words in L1 and L2. Admittedly, this study explores patterns in languages that are similar linguistically and focuses specifically on lexical processing in the L1 and L2. In previous studies of lexical search and retrieval using PET with Chinese–English bilingual subjects, we have shown our findings to generalize to very different languages (Klein et al., 1999). However, our results from previous studies on bilingual subjects have demonstrated that different aspects of language may be selectively impacted by delays in exposure to L2. We have observed activity in the left basal ganglia when L1 speakers of English have produced words in their L2, French (Klein et al., 1994, 1995, 2005), possibly due to greater articulatory demands required when producing words in L2 as compared to L1. Others have shown that bilingual subjects apply their L1 system to L2 processing. For example, Tan et al. (2003) showed that the lack of letter-to-sound conversion rules in Chinese led Chinese readers to be less capable of processing English by recourse to the analytic reading system on which English monolinguals rely. These types of results indicate that different aspects of language may be selectively affected by delays in exposure to L2 and that experience with one language may shape processing in a second language.

Future fMRI studies may shed light on the debate about the cerebral representation of the L2 by systematically varying age of acquisition, levels of L2 exposure and L2 proficiency since it is clear that these factors are critical (Moreno and Kutas, 2005; Proverbio et al., 2002). Nevertheless, our results provide some suggestion that proficiency level may play a larger role than age of acquisition in the cerebral representation of semantic processing in the L2, in line with the findings of Perani et al. (1998) and Wartenburger et al. (2003).

Acknowledgments

We thank Regina Visca, Sonja Huntgeburth and Mike Ferreira for technical help. Supported by grants from the Canadian Institutes of Health Research (CIHR), Natural Sciences and

Engineering Research Council of Canada (NSERC) and the Centre for Research on Language, Mind and Brain (CRLMB), McGill University.

References

- Belin, P., Zatorre, R.J., Hoge, R., Evans, A., Pike, B., 1999. Event-related fMRI of the auditory cortex. *NeuroImage* 10, 417–429.
- Binder, J.R., Frost, J.A., Hammeke, T.A., Cox, R.W., Rao, S.M., Prieto, T., 1997. Human brain language areas identified by functional magnetic resonance imaging. *J. Neurosci.* 17, 353–362.
- Burton, M.W., Small, S.L., Blumstein, S.E., 2000. The role of segmentation in phonological processing: an fMRI investigation. *J. Cogn. Neurosci.* 12 (4), 679–690.
- Callan, D.E., Jones, J.A., Callan, A.M., Akahane-Yamada, R., 2004. Phonetic perceptual identification by native- and second-language speakers differentially activates brain regions involved with acoustic phonetic processing and those involved with articulatory–auditory/orosensory internal models. *NeuroImage* 22, 1182–1194.
- Chee, M.W., Tan, E.W., Thiel, T., 1999a. Mandarin and English single word processing studied with fMRI. *J. Neurosci.* 19, 3050–3056.
- Chee, M.W., Caplan, D., Soon, C.S., Sriram, N., Tan, E.W., Thiel, T., Weekes, B., 1999b. Processing of visually presented sentences in Mandarin and English studied with fMRI. *Neuron* 23, 127–137.
- Chee, M.W., Hon, N., Lee, H., Soon, C., 2001. Relative language proficiency modulates BOLD signal change when bilinguals perform semantic judgements. *NeuroImage* 13, 1155–1163.
- Chee, M.W., Soon, C.S., Lee, H.L., 2003. Common and segregated neuronal networks for different languages revealed using functional magnetic resonance adaptation. *J. Cogn. Neurosci.* 15, 85–97.
- Chen, H.C., Leung, Y.S., 1989. Patterns of lexical processing in a non-native language. *J. Exper. Psychol., Learn., Mem., Cogn.* 15, 316–325.
- 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.
- Damasio, A., Damasio, H., 1992. Brain and language. *Sci. Am.* 267 (3), 88–95.
- de Groot, A.M.B., Dannenburg, L., van Hell, J.G., 1994. Forward and backward word translation. *J. Mem. Lang.* 33, 600–629.
- Dehaene, S., Dupoux, E., Mehler, J., Cohen, L., Paulesu, E., Perani, D., van de Moortele, P.F., Lehericy, S., le Bihan, D., 1997. Anatomical variability in the cortical representation of first and second language. *NeuroReport* 8, 3809–3815.
- Demb, J.B., Desmond, J.E., Wagner, A.D., Vaidya, C.J., Glover, G.H., Gabrieli, J.D.E., 1995. Semantic encoding and retrieval in the left inferior prefrontal cortex: a functional MRI study of task difficulty and process specificity. *J. Neurosci.* 15, 5870–5878.
- Demonet, J.F., Chollet, F., Ramsay, S., Cardebat, D., Nespoulous, J.L., Wise, R., Rascol, A., Frackowiak, R., 1992. The anatomy of phonological and semantic processing in normal subjects. *Brain* 115, 1753–1768.
- Desimone, R., 1996. Neural mechanisms for visual memory and their role in attention. *Proc. Natl. Acad. Sci. U. S. A.* 93, 13494–13499.
- Devlin, J.T., Matthews, P.M., Rushworth, F.S., 2003. Semantic processing in the left inferior prefrontal cortex: a combined functional magnetic resonance imaging and transcranial magnetic stimulation study. *J. Cogn. Neurosci.* 15, 71–84.
- de Zubicaray, G.I., Wilson, S.J., McMahon, K.L., Muthiah, S., 2001. The semantic interference effect in the picture–word paradigm: an event-related fMRI study employing overt responses. *Hum. Brain Mapp.* 14, 218–227.
- Fiez, J.A., 1997. Phonology, semantics, and the role of the left inferior prefrontal cortex. *Hum. Brain Mapp.* 5, 79–83.
- Grill-Spector, K., Malach, R., 2001. fMR-adaptation: a tool for studying the functional properties of human cortical neurons. *Acta Psychol.* 107, 293–321.
- Grill-Spector, K., Kushnir, T., Edelman, S., Avidan, G., Itzhak, Y., Malach, R., 1999. Differential processing of objects under various viewing conditions in the human lateral occipital complex. *Neuron* 24, 187–203.
- Hall, D.A., Haggard, M.P., Akeroyd, M.A., Palmer, A.R., Summerfield, A.Q., Elliot, M.R., Gurney, E.M., Bowtell, R.W., 1999. ‘Sparse’ temporal sampling in auditory fMRI. *Hum. Brain Mapp.* 7, 213–223.
- Hart Jr., J., Gordon, B., 1990. Delineation of single-word semantic comprehension deficits in aphasia, with anatomical correlation. *Ann. Neurol.* 27 (3), 226–231.
- Henson, R., Shallice, T., Dolan, R., 2000. Neuroimaging evidence for dissociable forms of repetition priming. *Science* 287, 1269–1272.
- Hernandez, A.E., Martinez, A., Kohnert, K., 2000. In search of the language switch: an fMRI study of picture naming in Spanish–English bilinguals. *Brain Lang.* 73, 421–431.
- Hernandez, A.E., Dapretto, M., Mazziotta, J., Bookheimer, S., 2001. Language switching and language representation in Spanish–English bilinguals: an fMRI study. *NeuroImage* 14, 510–520.
- Illes, J., Francis, W.S., Desmond, J.E., Gabrieli, J.D.E., Glover, G.H., Poldrack, R., Lee, C.J., Wagner, A.D., 1999. Convergent cortical representation of semantic processing in bilinguals. *Brain Lang.* 70, 347–363.
- Kim, K.H., Relkin, N.R., Lee, K.M., Hirsch, J., 1997. Distinct cortical areas associated with native and second languages. *Nature* 388, 171–174.
- 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., Milner, B., Zatorre, R.J., Zhao, V., Nikelski, J., 1999. Cerebral organization in bilinguals: a PET study of Chinese–English verb generation. *NeuroReport* 10, 2841–2846.
- Klein, D., Watkins, K., Zatorre, R.J., Milner, B., 2005. Word and nonword repetition in bilingual subjects: a PET study. *J. Hum. Brain Mapp.* (Jul 20; electronic publication ahead of print).
- Kotz, S.A., Cappa, S.F., von Cramon, D.Y., Friederici, A.D., 2002. Modulation of the lexical–semantic network by auditory semantic priming: an event-related functional MRI study. *NeuroImage* 17, 1761–1772.
- Kroll, J.F., Stewart, E., 1994. Category interference in translation and picture naming: evidence for asymmetric connections between bilingual memory representations. *J. Mem. Lang.* 33, 149–174.
- Moreno, E.M., Kutas, M., 2005. Processing semantic anomalies in two languages: an electrophysiological exploration in both languages of Spanish–English bilinguals. *Cogn. Brain Res.* 22, 205–220.
- Nobre, A.C., McCarthy, G., 1995. Language-related field potentials in the anterior–medial temporal lobe: II. Effects of word type and semantic priming. *J. Neurosci.* 15, 1090–1098.
- Paradis, M., 1989. Bilingual and polyglot aphasia. In: Boller, F., Grafman, J. (Eds.), *Handbook of Neuropsychology*, vol. 2. Elsevier, Amsterdam, pp. 117–140.
- Paradis, M. (Ed.), 1995. *Aspects of Bilingual Aphasia*. Pergamon Press, Oxford.
- Paradis, M., 1997. In: de Groot, A., Kroll, J. (Eds.), *Tutorials in Bilingualism: Psycholinguistic Perspectives*. Lawrence Erlbaum, pp. 331–354.
- Perani, D., Dehaene, S., Grassi, F., Cohen, L., Cappa, S.F., Dupoux, E., Fazio, F., Mehler, J., 1996. Brain processing of native and foreign languages. *NeuroReport* 7, 2439–2444.
- Perani, D., Paulesu, E., Galles, N.S., Dupoux, E., Dehaene, 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, 1841–1852.
- Pitres, A., 1895. Etude sur l’aphasie chez les polyglottes. *Rev. Méd.* 15, 873–899.

- Potter, M.C., So, K.-F., von Eckardt, B., Feldman, L.B., 1984. Lexical and conceptual representations in beginning and more proficient bilinguals. *J. Verbal Learn. Verbal Behav.* 23, 23–38.
- Phillips, N.A., Mercier, J., Klein, D., 2004. Semantic priming within and across languages: an auditory ERP study in bilinguals. Presented at the 44th Annual Meeting of the Society for Psychophysiological Research, Santa Fe, USA, October 20–24.
- Price, C.J., Green, D.W., von Studnitz, R., 1999. A functional imaging study of translation and language switching. *Brain* 122, 2221–2235.
- Proverbio, A.M., Cok, B., Zani, A., 2002. Electrophysiological measures of language processing in bilinguals. *J. Cogn. Neurosci.* 14 (7), 994–1017.
- Rinne, J.O., Tommola, J., Laine, M., Krause, B.J., Schmidt, D., Kaasinen, V., Teras, M., Sipila, H., Sunnari, M., 2000. The translating brain: cerebral activation patterns during simultaneous interpreting. *Neurosci. Lett.* 294, 85–88.
- Rodriguez-Fornells, A., Rotte, M., Heinze, H.J., Nössl, T., Münte, T.F., 2002. Brain potential and functional MRI evidence for how to handle two languages with one brain. *Nature* 415, 1026–1029.
- Schacter, D.L., Badgaiyan, R.D., 2001. Neuroimaging of priming: new perspectives on implicit and explicit memory. *Curr. Dir. Psychol. Sci.* 10, 1–4.
- Schacter, D.L., Buckner, R.L., 1998. Priming and the brain. *Neuron* 20, 185–195.
- Scott, S.K., Johnsrude, I.S., 2003. The neuroanatomical and function organization of speech perception. *Trends Neurosci.* 26, 100–107.
- Stowe, L.A., Paans, A.M., Wijers, A.A., Zwarts, F., Mulder, G., Vaalburg, W., 1999. Sentence comprehension and word repetition: a positron emission tomography investigation. *Psychophysiology* 36, 786–801.
- Talairach, J., Tournoux, P., 1988. *Co-Planar Stereotaxic Atlas of the Human Brain*. Thieme, New York.
- Tan, L.H., Spinks, J.A., Feng, C.M., Siok, W.T., Perfetti, C.A., Xiong, J.H., Fox, P.T., Gao, J.H., 2003. Neural systems of second language reading are shaped by native language. *Hum. Brain Mapp.* 18, 158–166.
- Vandenberghe, R., Price, C., Wise, R., Josephs, O., Frackowiak, R.S.J., 1996. Functional anatomy of a common semantic system for words and pictures. *Nature* 383, 254–256.
- Wagner, A.D., Koutstall, W., Maril, A., Schacter, D.L., Buckner, R.L., 2000. Task-specific repetition priming in left inferior prefrontal cortex. *Cereb. Cortex* 10, 1176–1184.
- Wagner, A.D., Pare-Blagoev, E.J., Clark, J., Poldrack, R.A., 2001. Recovering meaning: left prefrontal cortex guides controlled semantic retrieval. *Neuron* 31, 329–338.
- 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, 159–170.
- Wiggs, C.L., Martin, A., 1998. Properties and mechanisms of perceptual priming. *Curr. Opin. Neurobiol. (Cogn. Neurosci.)* 8, 227–233.
- Wise, R., Chollet, F., Hadar, U., Friston, K., Hoffner, E., Frackowiak, R., 1991. Distribution of cortical neural networks involved in word comprehension and word retrieval. *Brain* 114, 1803–1817.
- Worsley, K.J., Evans, A.C., Marrett, S., Neelin, P., 1992. A three-dimensional statistical analysis for CBF activation studies in human brain. *J. Cereb. Blood Flow Metab.* 12, 900–918.
- Worsley, K.J., Liao, C., Grabove, M., Petre, V., Ha, B., Evans, A.C., 2000. A general statistical analysis for fMRI data. *NeuroImage* 11, S648.
- 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.
- Zatorre, R.J., Evans, A.C., Meyer, E., Gjedde, A., 1992. Lateralization of phonetic and pitch discrimination in speech processing. *Science* 256, 846–849.
- Zatorre, R.J., Meyer, E., Gjedde, A., Evans, A.C., 1996. PET studies of phonetic processing of speech: review, replication, and reanalysis. *Cereb. Cortex* 6, 21–30.