

Language Control and Lexical Competition in Bilinguals: An Event-Related fMRI Study

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Language selection (or control) refers to the cognitive mechanism that controls which language to use at a given moment and context. It allows bilinguals to selectively communicate in one target language while minimizing the interferences from the non-target language. Previous studies have suggested the participation in language control of different brain areas. However, the question remains whether the selection of one language among others relies on a language-specific neural module or general executive regions that also allow switching between different competing behavioral responses including the switching between various linguistic registers. In this functional magnetic resonance imaging study, we investigated the neural correlates of language selection processes in German–French bilingual subjects during picture naming in different monolingual and bilingual selection contexts. We show that naming in the first language in the bilingual context (compared with monolingual contexts) increased activation in the left caudate and anterior cingulate cortex. Furthermore, the activation of these areas is even more extended when the subjects are using a second weaker language. These findings show that language control processes engaged in contexts during which both languages must remain active recruit the left caudate and the anterior cingulate cortex (ACC) in a manner that can be distinguished from areas engaged in intralanguage task switching.

Keywords: cognitive control, event-related functional magnetic resonance imaging, language selection, left hemisphere, picture naming, task selection

Introduction

The term bilingual refers to people who can use two languages (a native first language or L1, and a learnt second language or L2) in their everyday life. One of the fundamental features of the human bilingual brain is its capacity to control which language to use at a given moment and in a given context, both for speech comprehension and production. This specific cognitive mechanism, referred to as the “language control” or “language selection” mechanism, allows bilinguals, for instance, to communicate in one language rather than in another, and to switch back and forth between languages during the same conversation, depending on the preferred language of the interlocutors. It also allows to implicitly identify the language of heard or written words and to produce words in a selected target language, while minimizing the interferences from the nontarget language (e.g., by preventing prepotent interferences from the native L1 during production in a weaker L2).

Current cognitive models on bilingualism assume the existence of a single conceptual representation for the two languages that is linked to two different lexical representations, particularly in proficient and highly proficient bilinguals (De Groot and Kroll 1997; Francis 1999; Kroll and Stewart 1994). In this respect, implementing a communicative intention may then be an inherently competitive process in bilinguals (e.g., Gollan and Kroll 2001; Green 1998), given the need to restrict production to the preferred language of the listener. Thus, in order to communicate in one language and prevent unwanted interferences from the nontarget language, bilinguals have to actively select this target language and simultaneously inhibit (Green 1998) or raise the activation threshold (Grosjean 2001) of the nontarget language. However, the nature of the cognitive and neural mechanisms that allow bilinguals to select the appropriate language (referred to hereafter as the “language control” mechanism), and to deactivate the lexicon of the nontarget language is still a matter of debate.

Concretely, to what exactly does the notion of language control refer? Consider, for instance, the case of an English–French bilingual who has to retrieve the name “*chat*” (cat) during a picture-naming task in L2 (French). Will the word “*chat*” compete only with other L2 semantically related items, such as “*chien*” (dog), and “*souris*” (mouse), as well as with phonologically similar ones like “*chou*” (cabbage), or rather will the word “*chat*” also compete with L1 translation equivalents such as “cat,” and semantically related items such as “dog”? One possibility is that the lexical representations belonging to the nontarget language will not compete with those of the target language during lexical selection (Colomé 2001). Only lexical nodes (Costa and Caramazza 1999) or lemmas that meet the ongoing language goal (e.g., to speak in L2) will compete. The alternative possibility is that there will be competition between lemmas in different languages (e.g., De Bot and Schreuder 1993; Green 1986, 1998; Hermans et al. 1999; Lee and Williams 2001), which will be in general solved by inhibiting any active, nontarget language (Green 1998). The frequent occurrence of L1 interferences during the use of a weaker L2 (Grainger 1993; Grainger and Dijkstra 1992; Grosjean 1992) favors this latter view, which implies that both languages might remain active during speech production, and that language control in bilinguals is an implicit cognitive process.

This view finds a strong support in the study of bilingual aphasia. Case reports have shown that patients affected by left subcortical basal ganglia lesions, particularly of the caudate

nucleus, not only tend to involuntarily switch between their languages, but also show many interferences from the non-target language during naming tasks (Abutalebi et al. 2000; Marien et al. 2005). The pathological fixation to one language in bilingual aphasics (i.e., selective recovery of one language) after subcortical damage has also been interpreted in terms of impairment of the language control mechanisms (Aglioti and Fabbro 1993). Finally, other reports indicated that language switching difficulties may also be associated with lesions in the left prefrontal cortex (Fabbro et al. 2000) and in the left supramarginal gyrus (see Hernandez et al. 2001). Together, these neuropsychological observations led to the assumption that language control might rely on a left subcortical-cortical neural loop that comprises the caudate nucleus, the prefrontal cortex, and possibly the supramarginal gyrus.

Using various language paradigms, functional neuroimaging studies carried out in bilingual subjects have recently attempted to characterize the neural basis of language control processes. For instance, a positron emission tomography study on bilinguals performing translation and switching tasks based on visually presented words (Price et al. 1999) showed that switching between languages increased activation in Broca's area and the supramarginal gyrus. Translation conditions on the other hand increased activation in the anterior cingulate and basal ganglia structures. Language switching in picture naming (compared with nonswitching) increased functional magnetic resonance imaging (fMRI) responses in the right dorsolateral prefrontal cortex (Hernandez et al. 2001). Another fMRI study showed that, when controlling interference from the nontarget language during tacit naming in the target language, the bilingual subjects activated the left middle prefrontal cortex and the SMAs (Rodriguez-Fornells et al. 2005). Finally, using a semantic decision task in bilinguals, a recent functional imaging study reported activation in left caudate nucleus in relation to changes in the language in use, thus emphasizing the role of this structure in language control (Crinion et al. 2006).

Although the results of the studies outlined above might depend, at least partially, on the paradigms used, the emerging picture points to the involvement in language control of a set of left-lateralized brain areas, including the caudate nucleus, the prefrontal cortex, the anterior cingulate cortex, and the supramarginal gyrus. However, these areas are also known for their participation in other aspects of language processing (e.g., for the caudate and the prefrontal cortex, see Abutalebi et al. 2007; Friederici 2006; Gabrieli et al. 1998; Kapur et al. 1994; Lehericy et al. 2000; Price et al. 2005; Seghier et al. 2004; Warburton et al. 1996), as well as in other nonlinguistic selection tasks that require increased cognitive control and attentional demands (e.g., for the prefrontal cortex and the anterior cingulate cortex (ACC), see Botvinick et al. 1999; Brass et al. 2005; Braver et al. 2001; Carter et al. 1998, 2000; D'Esposito et al. 1995; Dreher et al. 2002; Friederici 2006; Graybiel 1997; Gruber and Goschke 2004; Nebel et al. 2005; Swainson et al. 2003). In this context, it is essential to disentangle regions that are specifically involved in language control/selection and which areas are activated by the specific task sets (Braver and Barch 2006; Dosenbach et al. 2006). In particular, it is still debated whether the cognitive mechanism that allows the selection of one language among others relies on a language-specific neural module or on general executive modules that are also involved in switching between various

competing behavioral responses including the switching from one linguistic register to another (Chee 2006).

The present study was designed to investigate the neural network underlying language control in bilinguals and to address the issue of the specificity of the language selection mechanism. For this purpose, we analyzed fMRI responses in bilingual subjects performing picture naming in two monolingual and one bilingual context. In the first monolingual simple naming context (SNc), images were presented on the computer screen and the subjects had to name them in L1. In the second monolingual task selection context (TSc), the subjects had either to name the image or to produce a related verb in L1 on the basis of a cue appearing immediately after each image. Finally, in the language selection context (LSc), subjects had either to name the image in L1 or in L2, again on the basis of a cue word appearing after each image. The analysis of functional responses aimed first at identifying the brain regions involved in picture naming. The TSc is thought to provide information on how subjects select the correct word form in their L1. The direct comparison of brain activity to L1 naming as a function of the selection context was designed to test whether the selection processes involved in LSc and TSc recruit different brain areas. The comparison of L2 naming and L1 naming in LSc sought to verify whether the same brain mechanisms involved in L1 selection are required when selecting words in the weaker L2.

Material and Methods

Subjects

Twelve healthy undergraduate bilingual students (10 females and two males, mean age = 25.4 ± 4.3 years) from the Translation department of the University of Geneva participated in the experiment and were reimbursed for their participation. All subjects were right-handed according to the Edinburgh Inventory (mean laterality index of 0.75 ± 0.14) and had German as their first language (L1) and French as second language (L2). All subjects had normal or corrected-to-normal vision and none had a history of neurological or psychiatric diseases. As recommended by the research ethical committee of the Geneva University Hospitals, they all provided a formal written consent for participating to this study.

Language Proficiency Assessment

All subjects followed school in German since their early childhood and started learning French as their L2 on average at the age of 11.6 ± 1.2 years. Before admission to translation studies at the university, they had all passed the university examination with French as second language. At the time of this investigation, all but two had completed with success their second year studies (out of four) and were already enrolled in the third year. Prior to the experiment, they had all completed a questionnaire assessing the amount of actual exposure to languages in areas including media, family, university, friends, girlfriend/boyfriends, reading, and other activities (e.g., hobbies, sports, music, etc., see for details Wartenburger et al. 2003). This assessment allows having an approximation of the overall actual exposure to a given language. On average their responses indicated that they were exposed to L1 for 4.5 ± 1.5 h and to L2 for 6 ± 4 h per day for the daily activities investigated.

The level of proficiency in L2 was also assessed by means of a translation test that evaluates the quality of translation from L2 to L1, as index of proficiency. The text to be translated from L2 into L1 was about 150 words long without time constraint, although all the keyboard activity was continuously tracked by the computer software used (TRANSLOG2000; <http://www.translog.dk>). The analysis of the translation quality, as evaluated by two independent professional raters, indicated that the scores were quite high among the group (mean = 53

± 10 out of 80) and attested of their good proficiency in L2. In addition, and despite the absence of time constraint to perform the test, the total translation times were homogenous across subjects (30 ± 7 min), except in one who showed an extremely short translation time (15 min). Finally, we also considered the subjects' performance in L2 naming condition as an index of their proficiency level in this language (see below).

Stimuli and Procedures

The subjects performed a picture naming in two monolingual (L1) and in one bilingual contexts. For minimizing the possible interference of the bilingual on the monolingual mode (see for details Grosjean 2001), all subjects were first tested in the monolingual contexts and then in the bilingual one. More important from the hemodynamic view, the reason to start with the monolingual context was due to the well-known "neuronal habituation" effects in functional neuroimaging (see Donaldson and Buckner 2001). Because our a priori hypothesis (based upon previous fMRI evidence such as the studies of Hernandez et al. 2001) was that the bilingual context would lead to greater overall brain activity, it would have been difficult to exclude an habituation effect for the eventual observation of less activity for the monolingual contexts (i.e., if these latter would have been presented after the bilingual context). In the first monolingual context, referred to as SNC, the images were presented on the computer screen and for each image the subjects had to give the name in L1. In the second monolingual context, referred to as TSc, the subjects were presented with images and on the basis of a cue word that followed immediately each image, they had either to give the name in L1 or to produce a related verb in L1. This context, carried out in L1 only, was thought to provide information on how subjects select the correct word form within their first language. Finally, in the third, bilingual context, here referred to as LSc, the subjects had, on the basis of a cue word that followed immediately each image, to generate the name either in L1 or in L2. This naming task, performed in a highly mixed bilingual context, is hypothesized to provide information, first on whether the selection process for L1 nouns is different from that involved during TSc, and second whether there are differences between selecting L1 and L2 items.

For the three contexts, we used a total of 175 different black and white drawings. These stimuli (of 8.5×8.5 cm each) represented only manufactured objects (tools, furniture, clothes, kitchen objects, electric apparatus, vehicles, etc.) and were selected from two different databases (Cycowicz et al. 1997; Snodgrass and Vanderwart 1980). In the SNC, the stimuli consisted of a total of 35 different images, each repeated once in a single run of 70 randomly distributed stimuli. In the TSc context, the stimuli consisted of total of 70 other different images that were all presented in two successive experimental runs. In the first experimental run of TSc, half of the images ($n = 35$) were pseudorandomly cued for verb generation, and the other half for naming in L1. The second stimulation run used again the same 70 stimuli as in the first run but the images cued in the first run for verb generation were now presented for L1 naming and those used for L1 naming were now presented for verb generation. Accordingly, this provided a total of 140 trials (each of the 70 images repeated once) of which 70 trials for verb generation and 70 for L1 naming. In the LSc context, another new set of 70-matched images was again presented in a similar two-run design, again with each image repeated once and yielding thus a total of 140 trials. Thus, in the first run, half of the images ($n = 35$) were pseudorandomly presented for L1 naming and the other half ($n = 35$) for naming in L2. In the second run, the first half of the images was now used for L2 naming and the second half for naming in L1. In each of these two-run designs (i.e., TSc and LSc), the order of the experimental runs was balanced over subjects and the different conditions (verb generation vs. L1 naming in TSc and L1 vs. L2 naming in LSc) within each experimental run were differently randomized for each subject. In the whole, the experimental paradigm consisted of five distinct runs: one run for the L1 SNC, two runs for L1 TSc, and two runs for the bilingual LSc. All images used in the three contexts were comparable in terms of visual complexity (mean complexity = 2.8, 2.9, and 3.0, respectively, in SNC, TSc, and LSc) based on norms for adults (Alario and Ferrand 1999). Furthermore, word frequency analysis based, respectively, on German (Genzel et al. 1995) and French norms

(Content et al. 1990) showed that in both languages the words were on the average of middle to high lexical frequency (mean CELEX for German nouns, respectively = 155, 187, and 199, respectively, in SNC, TSc, and LSc and mean CFLEX = 317 for the French nouns of the same images in LSc). Word agreement for nouns and verbs was analyzed on the basis of the subjects' individual responses to each single item in each condition (see the Behavioral results section).

In all contexts, each stimulation trial whose duration was of 4, 5, or 6 s started with a fixation cross that appeared centrally and lasted for 1 s. The stimulus image was then displayed centrally for 150 ms. Immediately after the image, and in order to preclude possible subvocal automatic repetition of the image name (particularly in the TSc and the LSc), a "cue" word was presented for 300 ms to induce the subject's response to the present trial. In the monolingual L1 SNC, the cue word was "NAME." In the monolingual L1 TSc the cue word was either "NAME" or "VERB." In the bilingual LSc, and in order to avoid any confusion between the word "name" in German and the word "nom" in French, the cue word indicated directly the language to use: that is, "DEUTSCH" for L1 naming and "FRANÇAIS" for L2 naming. A blank screen of either 2550, or 3550 or 4550 ms (respectively, for trials of either 4, 5, or 6 s duration) followed the cue to allowing subjects' responses. The appearance afterwards of the central fixation cross announced the occurrence of the following trial. For all conditions, the subjects were asked to give an overt oral response as quietly as possible without moving their heads (Heim et al. 2006). For minimizing the experimental constraints during MRI acquisition, the subjects' actual responses and the time of voice onset relative to the image-offset was collected and analyzed from a separate behavioral session. However, in order to qualitatively control the subject's responses during each acquisition run, they were informed that their responses were continuously recorded using the interphone device.

fMRI Acquisition

Experiments were performed on a 1.5-T system (Philips Medical Systems, Best, The Netherlands). Acquired multislice volume was positioned on sagittal scout images. Functional imaging consisted of an echo planner imaging with gradient echo (EPI GRE) sequence (time repetition [TR]/time echo [TE]/Flip = 2 s/40 ms/80°, field of view (FOV) = 250 mm, matrix = 128×128 , in-plane resolution = 1.95×1.95 , 23 contiguous 4-mm axial slices). Each scan was repeated 210 times leading to a total acquisition duration of 7 min by experimental run. For each run, the functional scanning was always preceded by 8 s of dummy scans to insure tissue steady-state magnetization. Anatomical reference images, acquired after the functional scans, consisted of a 3-D GRE T_1 -weighted sequence (TR/TE = 15 ms/5 ms, FOV = 250 mm, matrix = 256×256 , slice-thickness = 1.25 mm). A vacuum cushion (PAR Scientific A/S, Denmark) was used to minimize head movement.

Image Processing and Statistical Analysis

Data processing and statistical analyses were carried out with Statistical Parametric Mapping SPM2 software package (Wellcome Trust Centre for Neuroimaging, London UK, <http://www.fil.ion.ucl.ac.uk/spm/>). All functional volumes were spatially realigned, corrected for slice timing, normalized to the Montreal Neurological Institute (MNI) space, and smoothed with an isotropic 6-mm full width at half-maximum (FWHM) Gaussian kernel. The resulting voxels size after normalization was $2 \times 2 \times 2$ mm³. Time-series from each voxel were high-pass filtered (1/128 Hz cutoff) to remove low-frequency noise and signal drift. For each subject, the preprocessed functional volumes were then submitted to fixed-effects analyses (i.e., first level analysis) using the general linear model applied at each voxel across the whole brain. Each stimulus onset (activation and control conditions) was modeled as an event encoded in condition-specific "stick-functions." The resulting stimulus functions were convolved with a canonical hemodynamic response function (with no dispersion or temporal derivatives) and included in a multiple regression analysis with six covariates of no interest representing the head motion parameters (Friston et al. 1996; Johnstone et al. 2006). The effects of the experimental design were assessed on a voxel-by-voxel basis using the General Linear Model. The simple main effects and the direct comparisons between the conditions

were performed on a second level analysis (random effects) at $P < 0.005$ (uncorrected) in order to generalize the results from our sample to the population (Friston et al. 1999). We furthermore performed an ANOVA based conjunction analysis between different conditions at $P < 0.001$ uncorrected (see for more details Price and Friston 1997). An extent threshold of 10 contiguous voxels was applied to all contrasts.

From the second level analysis, the following statistical contrasts were computed: 1) a conjunction analysis between all L1 naming conditions in order to detect areas common to picture naming across contexts (i.e., SNC, TSc, and LSc); 2) a conjunction analysis between L1 naming in the TSc and L1 naming of the LSc in order to identify areas common to selection across contexts; 3) a direct comparison between the L1 naming of the monolingual TSc versus SNC; 4) a direct comparison between L1 naming of the bilingual LSc versus the monolingual SNC; 5) a direct comparison between L1 naming of the bilingual LSc versus the monolingual TSc; 6) a direct comparison between L2 naming and L1 naming (and vice versa) in the LSc. All the coordinates derived from the statistical analysis were converted from MNI to Talairach and Tournoux stereotaxic space (Talairach and Tournoux 1988).

Results

Behavioral Results

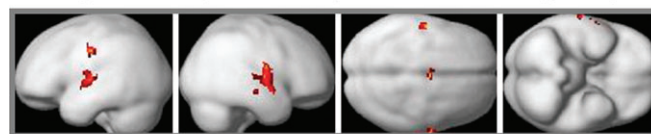
The analysis of the subjects' rate of correct responses for L1 naming in the different contexts (SNC, TSc, and LSc) using a 1×3 ANOVA showed that their performance did not differ across contexts ($F_{2,22} = 0.8$, $P = 0.48$, mean rate of correct responses \pm SD = 96 ± 2 , 96 ± 2 , and $95 \pm 3\%$, respectively, for SNC, TSc, and LSc). Word agreement in these three naming conditions was on the average of 91 ± 15 , 86 ± 18 , and $85 \pm 19\%$, respectively, in SNC, TSc, and LSc. In terms of response speed, a similar analysis on the reaction times (RTs) (relative to the cue word) showed a highly significant context effect ($F_{2,22} = 80.8$, $P < 0.000001$). Post hoc Scheffe tests showed that this effect was because responses in the SNC (759 ± 96 ms) were much faster than in TSc (1117 ± 145 ms, $P < 0.000001$) and in LSc (1156 ± 130 ms, $P < 0.000001$), whereas the latter two did not differ ($P < 0.53$). In the monolingual TSc, the analysis of subjects' performance showed a mean correct response rate of $95 \pm 3\%$ in verb generation and of $96 \pm 2\%$ in L1 naming ($P = 0.6$). In terms of RT, verb generation condition took longer time than L1 naming (mean = 1202 ± 144 and 1117 ± 145 ms, respectively; $t = 4.1$; $P < 0.002$; $df = 11$). Similarly, word agreement for each image showed a higher percentage of agreement for names ($86 \pm 18\%$) than for verbs ($67 \pm 23\%$). In the bilingual LSc, subjects' performance was as expected higher in L1 ($95 \pm 3\%$) than in L2 ($85 \pm 10\%$, $t = 4.4$; $P < 0.001$; $df = 11$). In contrast, this specific context showed that RTs to L1 naming did not differ from those to L2 naming (respectively = 1156 ± 130 and 1196 ± 170 ms, $P = 0.29$). No significant difference was found for word agreement in L1 ($85 \pm 19\%$) and L2 names ($84 \pm 20\%$).

Neuroimaging Results

Conjunction Analysis

The conjunction analysis performed on the L1 naming condition across the three different contexts (i.e., L1 naming in the SNC, the TSc and the LSc), revealed a bilateral pattern of brain activation. As illustrated in Fig. 1(A) and detailed in Table 1, the areas activated included the dorsal frontal gyrus (or the supplementary motor area; SMA), the left precentral gyrus, the anterior superior temporal gyrus bilaterally, and the right anterior middle temporal gyrus. The conjunction analysis

A Conjunction analysis: L1 naming in SNC, TSc and LSc ($p < 0.001$)



B Conjunction analysis: L1 naming in TSc and LSc ($p < 0.001$)

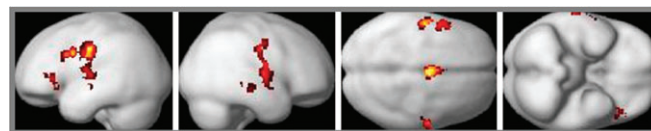


Figure 1. (A) The group activation map (at $P < 0.001$) as revealed by the conjunction analysis between L1 naming in the SNC, TSc, and LSc. (B) The group activation map as revealed by the conjunction analysis between L1 naming in the TSc and the LSc (see the anatomical localization and coordinates in Table 1).

Table 1

Anatomical localization of brain activity revealed by the conjunction analyses

Statistical analysis and anatomical location	Coordinates (x; y; z)	Z-value	Brodman area
(a) Conjunction between L1 naming in SNC, TSc and LSc			
L dorsal frontal gyrus (SMA)	-2; -4; 60	3.71	6
L precentral gyrus	-56; -12; 38	3.45	6
L anterior superior temporal gyrus	-62; -8; 4	3.48	22
R anterior superior temporal gyrus	58; -6; 4	3.36	22
R anterior middle temporal gyrus	60; -12; -8	3.47	21
(b) Conjunction between L1 naming in TSc and LSc			
L inferior frontal gyrus	-42; 28; 4	4.70	45
—	-46; 26; -8	3.65	47
—	-48; 14; 28	4.38	44
L dorsal frontal gyrus (SMA)	-2; -4; 60	5.90	6
L precentral gyrus	-52; -12; 36	5.34	6
L anterior middle temporal gyrus	-62; -14; -6	3.61	21
L thalamus	-8; -6; 8	3.64	—
R precentral gyrus	44; -16; 32	5.34	6
R anterior superior temporal gyrus	64; -6; 8	4.63	22
R anterior middle temporal gyrus	70; -24; -12	3.83	21
R middle temporal gyrus	56; -32; -2	3.33	21

Note: Anatomical localization of brain activity (at $P < 0.001$) as revealed by (a) the conjunction analysis between L1 naming in the three contexts, that is SNC, TSc, and LSc; and (b) the conjunction analysis between L1 naming in the TSc and LSc. In this and the following tables, L refers to left hemisphere and R to right hemisphere. Note also that here and in the following tables, and as a function of the size of the activated area, some of the regions are reported several times in order to account for the extension of the functional responses.

performed on the L1 naming across the two selection contexts (i.e., TSc and LSc) entailed a more extended pattern of brain activity. In the left hemisphere (LH), the activation involved antero-posteriorly the inferior frontal gyrus (BA 45 and 47), including the pars opercularis the inferior frontal gyrus (BA 44), the SMA, the precentral gyrus, the anterior middle temporal gyrus, and the thalamus. In the right hemisphere (RH), the activation was found in the precentral, the anterior superior, and the middle temporal gyri (see Table 1 and Fig. 1B).

Direct Comparisons of L1 Naming in the Different Contexts

The direct comparisons performed first between the L1 naming of the TSc and the SNC, and then between the L1 naming of the LSc and the SNC aimed at characterizing brain activity related to intralanguage and interlanguage selection processes. As shown in Fig. 2 and detailed in Table 2, both comparisons revealed

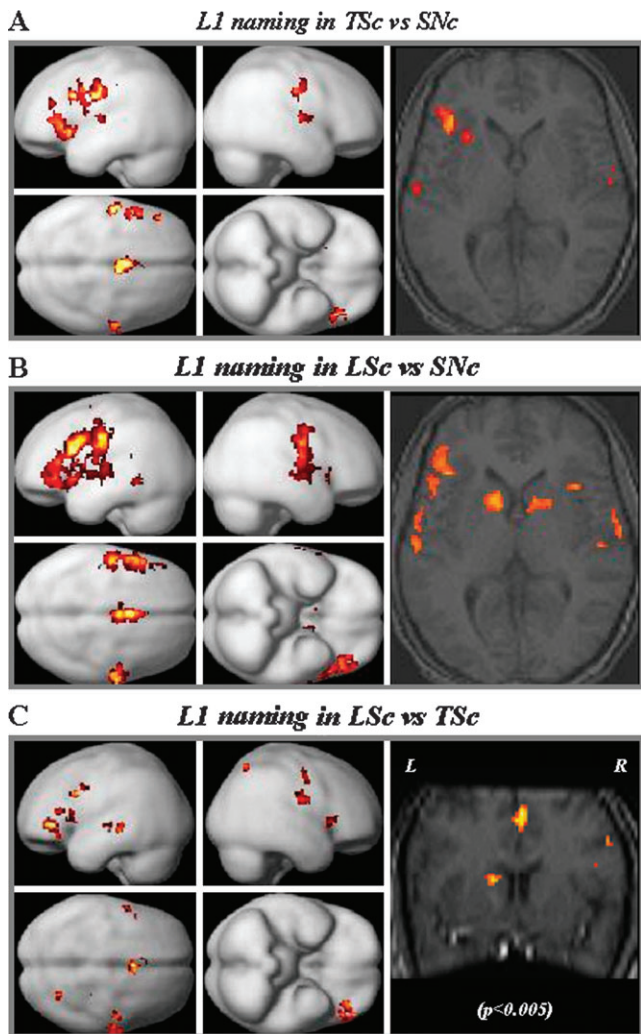


Figure 2. (A) The group activation map (at $P < 0.005$) as revealed by the direct comparison of L1 naming in the TSc versus the SNc. (B) Direct comparison of L1 naming in the LSc versus the SNc. (C) Direct comparison of L1 naming in the LSc versus the TSc. The axial slices in (A) and (B) are shown to illustrate the activation of the caudate nucleus in LSc but not in TSc. The coronal slice in (C) illustrates the specific activation in LSc of the left anterior cingulate cortex and the left caudate nucleus. Note that the all slices presented here and in the next figure are in the neurological convention (see the anatomical localization and coordinates in Table 2).

a LH-dominant pattern of activation. In the former comparison, LH responses were found in the inferior frontal gyrus (BA 44, 45, and 47) including the pars opercularis BA, in the middle frontal gyrus (BA 9 and BA 46), the SMA, the precentral gyrus, and the anterior part of the superior temporal gyrus (BA 22). In the RH, the activation involved the precentral gyrus, the SMA, the anterior cingulate cortex, and the anterior superior temporal gyrus (Table 2 and Fig. 2A).

Interestingly, the direct comparison between L1 naming in LSc versus SNc (Fig. 2B and Table 2), revealed a larger neural network than in the former comparison but included almost all the areas found before. In detail, brain activity found in the left frontal lobe extended more rostrally along the inferior frontal gyrus and the middle frontal gyrus (see Fig. 2B). In addition, other LH activations were found in the anterior cingulate cortex (BA 24), the posterior superior temporal gyrus (BA 22), the middle temporal gyrus (BA 21), and the caudate nucleus. In

Table 2

Localization of brain activity in L1 naming as a function of the context

Statistical analysis and anatomical location	Coordinates (x; y; z)	Z-value	Brodman area
(a) Comparison of L1 naming in TSc versus SNc			
L inferior frontal gyrus	-40; 28; 2	3.93	45
	-44; 28; 10	3.52	45
	-52; 4; 24	3.84	44
	-40; 18; -8	3.75	47
L middle frontal gyrus	-54; 16; 32	4.04	9
	-46; 36; 24	3.41	46
L dorsal frontal gyrus (SMA)	-2; 2; 60	4.24	6
L precentral gyrus	-58; -6; 30	4.52	6
	-46; -6; 30	4.21	6
L anterior superior temporal gyrus	-64; -12; 8	3.55	22
R dorsal frontal gyrus (SMA)	6; -4; 60	4.45	6
R precentral gyrus	44; -16; 32	4.85	4/6
	64; -8; 34	3.11	6
R anterior cingulate cortex	10; 14; 36	4.65	32
R anterior superior temporal gyrus	62; -10; 6	3.47	22
(b) Comparison of L1 naming in LSc versus SNc			
L inferior frontal gyrus	-44; 14; 22	4.67	44
	-48; 24; 16	3.95	45
	-50; 32; 0	4.25	47
L middle frontal gyrus	-42; 10; 32	4.51	9
L dorsal frontal gyrus (SMA)	-2; -4; 62	4.61	6
L anterior cingulate cortex	-6; 10; 32	4.51	24
L precentral gyrus	-52; -12; 36	5.10	6
L posterior superior temporal gyrus	-46; -40; 18	3.78	22
L middle temporal gyrus	-50; -46; -6	3.45	21
L caudate nucleus	-16; 6; 6	3.89	—
	-8; 2; 0	3.88	—
R inferior frontal gyrus	38; 20; 6	3.49	45
R dorsal frontal gyrus (SMA)	2; 8; 52	5.10	6
R precentral gyrus	46; -4; 32	4.12	6
R anterior superior temporal gyrus	54; -18; 0	3.69	22
R caudate nucleus	16; 8; 12	3.38	—
(c) Comparison of L1 naming in LSc versus TSc			
L inferior frontal gyrus	-50; 32; -2	4.47	47
	-46; 28; 14	3.95	45
	-48; 16; 10	3.92	44
L superior frontal gyrus (SMA)	-10; 22; 50	4.06	6
L dorsal frontal gyrus (SMA)	-2; 10; 54	4.91	6
L anterior cingulate cortex	-16; 34; -4	3.82	24
	-16; 24; -4	3.76	24
L middle temporal gyrus	-56; -30; -4	3.80	21
L caudate	-18; 0; 22	4.01	—
	-16; 8; 14	3.82	—
R inferior frontal gyrus	40; 18; 0	4.22	47
R precentral gyrus	38; 0; 54	4.36	6
	42; -12; 28	3.75	6
R superior parietal lobule	24; -62; 60	3.74	7

Note: Anatomical localization of brain activated areas (at $P < 0.005$, with their xyz coordinates and the highest Z-values) as revealed in the direct comparison of: (a) L1 naming in task selection (TSc) versus SNc; (b) L1 naming in language selection (LSc) versus SNc and (c) L1 naming in LSc versus TSc. Note that grey highlights in (b) and (c) indicate the major difference between these comparisons and the first (a).

the RH, additional activations were also found in the inferior frontal gyrus and the caudate nucleus (see Table 2).

These differences were confirmed by the direct comparison between L1 naming in LSc versus TSc. Indeed, like the former comparison, this one also showed the involvement in the LH of the anterior cingulate cortex (BA 24), the middle temporal gyrus (BA 21), and the caudate nucleus (see Fig. 2C and Table 2). In the RH, other activations were additionally found in the inferior frontal gyrus and the superior parietal lobule.

Direct Comparisons of L2 and L1 Naming

The direct comparison between the two languages (L2 vs. L1 and L1 vs. L2) in the LSc revealed striking differences. Actually, contrasting L2 to L1 naming showed the recruitment of

a relatively extensive network mainly dominated by the large activation of the left cingulate cortex which extended most rostrally from $x = -6, y = 32, z = 20$ to $x = -2, y = -22, z = 38$ most caudally (see Fig. 3 and Table 3). Other foci of brain activity were also found within the LH, including the inferior frontal gyrus (BA 44, 45, and 47), the middle frontal gyrus (BA 10/46), the precentral gyrus, and the caudate nucleus which all have been found in the former comparisons (Table 2). In the RH, the differences were located in the anterior cingulate cortex, the dorsal frontal gyrus (BA 9), the putamen, and caudate nucleus. In contrast, the comparison between L1 and L2 naming revealed brain activity only in the right inferior parietal lobule (Table 3).

Discussion

The main aim of the present study was to determine whether brain mechanisms allowing the selection of a target language differ from those involved in general executive functions that control the switching between various competing behavioral registers. We achieved this goal by investigating bilingual subjects in different selection contexts.

Our results indicate first that when bilinguals are placed in a mixed bilingual context there is greater engagement of brain structures putatively involved in cognitive and language control mechanisms. Indeed, as shown by the direct comparison of L1 naming in the bilingual LSc and L1 naming in monolingual TSc, these brain structures are mainly represented by the left ACC and the left caudate. Second, we have shown that activation in some of these structures is even more important when it comes to the task of selecting the less dominant language as shown by the direct comparison between L2 and L1 naming in the LSc. These two aspects will be discussed in detail.

Bilingual Language Context versus Single Language Context

To investigate the neural correlates of the supposed cognitive differences between two different language contexts, we compared brain activity induced by the same L1 naming condition as a function of the selection context: a monolingual TSc and a bilingual LSc. Our rationale was that if selecting

a lexical item in L1 in the bilingual context differs from the monolingual selection context, then brain activity should differ between these two (otherwise exactly similar) L1 naming conditions. Unlike other designs that manipulate language switching with a predictable task sequence (Rogers and Monsell 1995) in order to assess switching costs (Jackson et al. 2001; Swainson et al. 2003), the presentation here of the different conditions in each context was randomized for each subject, on the basis of a trial-by-trial cuing without any predictable order. The random naming in L1 and L2 was crucial for creating a totally mixed bilingual context, in which language selection takes place, which could be then contrasted to a comparable intra-language task selection context.

At the behavioral level, performance analysis in L1 naming showed that the rate of correct responses did not differ between contexts. In terms of reaction times (RTs), our analysis showed that L1 naming was significantly shorter in the SNC as compared with TSc and LSc, whereas the later two contexts were not different. Compared with the L1 naming in the SNC (i.e., without any selection process), the additional time for L1 naming in TSc and LSc was partially due to the selection costs, but also to the fact that in the latter two contexts the subjects had to wait and process the cue word before responding. This finding is in line with previous results showing that switching, which is a time-consuming process, will delay response selection if it occurs after target presentation (Swainson et al. 2006). However, compared with other studies using naming tasks, the RTs measured here were considerably longer than those reported for instance by Hernandez et al. (2001). In the latter study, the cue indicating the language in which to produce the name was presented before the images. Indeed, presenting a cue before the lexical item is thought to abolish costs related to in-between language selection processes because selection is limited only to items within a single language specific lexicon, hence resembling a process identical to word production in monolinguals (see

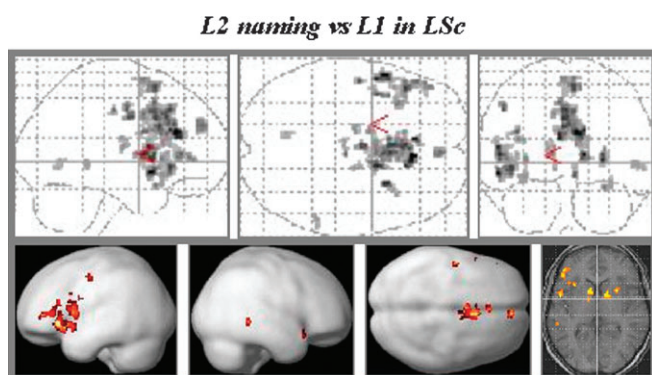


Figure 3. The group activation map (at $P < 0.005$) as revealed by the direct comparison of L2 versus L1 naming in the LSc. The sagittal, axial, and coronal views of the glass brain in the upper row are shown to illustrate the extension of activation in the left anterior cingulate cortex and the left inferior frontal gyrus. The axial MR slice in the lower row illustrates the activation in the caudate nucleus bilaterally (see the anatomical localization and coordinates in Table 3).

Table 3

Localization of brain activity in L2 versus L1 and L1 versus L2 naming

Statistical analysis and anatomical location	Coordinates (x; y; z)	Z-value	Brodman area
(a) Comparison of L2 versus L1 naming in LSc			
L inferior frontal gyrus	-54; 14; -8	4.20	47
	-44; 26; -4	3.89	47
	-50; 34; 6	3.60	45
	-54; 8; 12	4.03	44
	-38; 12; 26	3.35	44
L middle frontal gyrus	-46; 44; 2	3.32	10/46
L anterior cingulate cortex	-6; 32; 20	4.03	32
	-2; 26; 42	3.90	32
	-2; 14; 34	3.90	24
	-2; -8; 36	3.79	24
L posterior cingulate gyrus	-2; -22; 38	3.02	31
L precentral gyrus	-50; -10; 42	3.70	6
L caudate nucleus	-10; 4; 4	3.93	—
R superior frontal gyrus	4; 52; 28	3.50	9
R dorsal frontal gyrus (SMA)	4; 14; 60	3.81	6
R anterior cingulate cortex	8; 30; 24	4.35	32
R caudate nucleus	14; 4; 6	4.03	—
R putamen	30; 14; 10	3.33	—
(b) Comparison of L1 versus L2 naming in LSc			
R inferior parietal lobule (angular gyrus)	44; -60; 38	4.09	40

Note: Activated brain regions (at $P < 0.005$, with the xyz coordinates and the highest regional Z-values) as revealed by the direct comparison between L2 versus L1 naming (a) and between L1 versus L2 (b) in the LSc.

Grosjean 2001) for a definition of monolingual mode in bilinguals). Based on psycholinguistic evidence proposing that bilinguals have common semantic representations that are linked to two different lexical representations (De Groot and Kroll 1997; Francis 1999; Kroll and Stewart 1994), we assume here that the subjects had first to enter the semantic system and then language selection took place (with the eventual inhibition of the nontarget language). Thus, if competition occurs, it should occur only at the lexical level. Note also that, because of the differences in the experimental paradigms, it is also difficult to compare our study with other functional neuroimaging studies carried out with bilinguals (i.e., word translation and word switching: Price et al. 1999; sentence translation: Lehtonen et al. 2005; pre-cued naming: Hernandez et al. 2001; go/no-go tacit picture-naming task: Rodriguez-Fornells et al. 2005; and semantic decision task: Crinion et al. 2006).

Regarding the neural structures engaged during the two selection contexts, the conjunction analysis showed that the selection of L1 names, independent of the context (Fig. 2B and Table 2), entailed increased activation in several language-related areas, particularly the left inferior frontal gyrus (BA 47 and BA 45), and the superior and middle temporal gyrus bilaterally, but also the bilateral precentral gyrus, the SMA and the left thalamus. The involvement of these areas in various aspects of language production and comprehension is well documented by functional imaging studies and will thus not be discussed here (see references for instance in Bookheimer 2002; Seghier et al. 2004 for semantic and phonological processing, in Friederici 2002 for syntactic processing and in Christoffels et al. 2007; Ellis et al. 2006; Saccuman et al. 2006 for covert and overt naming tasks).

When compared with a simple L1 naming task (SNc), L1 naming in both selection contexts (TSc and LSc) activated more anterior parts of the left frontal lobe such as the middle frontal gyrus (BA 9 and 46) and, more extensively, the inferior frontal gyrus (BA 45 and 47, Fig. 2 and Table 2). This finding may be related to the specific processing demands inherent to lexical retrieval following a cue. As frequently observed in neuroimaging studies in monolinguals (see Thompson-Schill et al. 1997, 1999) the activity observed in the left inferior and middle frontal gyri (BA 9, 46, and 47) may be related to selection processes between competing alternatives (Rodriguez-Fornells et al. 2005). Concerning more precisely BA 46, we observed that this middle frontal area was activated exclusively in the comparison of L1 naming in TSc versus SNc. In view of this observation, one can thus suggest that BA 46, repeatedly involved in executive functioning such as the selection of different response alternatives (D'Esposito et al. 1995), and the switching between tasks (Dreher et al. 2002; Rodriguez-Fornells et al. 2005), is not mandatory for language selection. Furthermore, the implication of either the two different parts (i.e., BA 46 and BA 9) or only one part (BA 9) of the middle frontal gyrus is in line with the functional segregation proposed in this region by Petrides et al. (1993) for working memory functions and extended to the language domain (Seghier et al. 2004). In view of this hypothesized segregation, it is worth reminding that although BA 46 was activated together with the BA 9 in the TSc versus SNc comparison, only BA 9 was observed in the LSc versus SNc contrast (but not in the LSc versus TSc, see Table 2), suggesting thus that this latter area might have been involved in both types of selection processes.

Moreover, the production of L1 names in the LSc versus SNc induced activation in the left ACC and the caudate nucleus. The left ACC and caudate were also found in the direct comparison between the L1 naming in LSc versus TSc. This finding strongly suggests that the cognitive processes underlying lexical retrieval might differ between the two selection contexts. However, it should be underlined that these findings may not only be related to processing demands inherent to lexical retrieval (i.e., lexical competition in the specific case) because it is possible that in the LSc there may be less lexical alternatives with whom to compete (i.e., the word and a small amount of translation equivalents), whereas there may be more alternatives in the TSc (the word, a large amount of L1 alternatives and L1 verbs). Having more alternatives to compete with would lead to greater engagement of the left inferior frontal cortex (Thompson-Schill et al., 1997). However, the more extended engagement of this region was found in the LSc (along with the specific engagement of the caudate and ACC) (see Table 2). On the one hand, these data suggest that, in a bilingual condition, competition is particularly prominent (even with a limited amount of competitors) and, on the other, the activity is inherent to bilingual language processing: the need of inhibiting the nontarget language and to activate the target language.

This latter hypothesis supports cognitive models suggesting that, when placed in a language context where they potentially have to use both languages, bilinguals might be in need of a cognitive mechanism that prevents interferences from the nontarget language (Green 1986, 1998; Grosjean 2001; Hermans et al. 1999; Kroll et al. 2006; Lee and Williams 2001). Previous studies have already proposed that the ACC and the left caudate (Abutalebi and Green 2007) may subserve such a cognitive mechanism at the brain level. In particular, it is well known that the ACC is considerably involved in cognitive control (Bush et al. 2000; Cabeza and Nyberg 1997). Likewise, the caudate nucleus with its multiple parallel excitatory and inhibitory cortical connections is crucially implied in cognitive control and information processing (Graybiel 1997; Middleton and Strick 2000). With respect to language production, the left caudate may subserve language planning (Fabbro et al. 1997) through a left caudate-left prefrontal cortex circuitry. Recent work carried out to disentangle the role of the caudate from that of the prefrontal cortex has proposed the prefrontal cortex to be involved in maintaining representations in the face of competing interference, whereas the caudate has a more direct role in the inhibition of inappropriate behaviors (Casey et al. 2001) and in error control (Lawrence 2000). Damage to this subcortical-cortical circuitry may give rise not only to interferences from the nontarget language during naming tasks but also to pathological language switching in bilinguals (Abutalebi and Green 2007; Abutalebi et al. 2000; Marien et al. 2005) because of loss of control over the bilinguals language systems. Following Chee (2006), the sensitivity of the caudate to language switching might reflect its role in classifying the stimuli to ensure contextually meaningful language output (for instances, to respond with the target language). Hence, the left caudate may mediate the selection of words in one language rather than another or, in the words of Crinion et al. (2006), "monitoring and controlling the language in use."

In this context, our findings are striking insofar as it was postulated that such a cognitive mechanism might be much more needed when it comes to the task of inhibiting the

dominant language (L1). Actually, psycholinguistic models (Green 1998) assume that, in order to prevent unwanted L1 interferences, the inhibition process applied on L1 words will be stronger (and thus higher switching costs are required to overcome it) during word production in the weaker L2. However, in the present study the dominant language was L1, and nevertheless we observed the engagement of these structures (the left ACC and caudate) that are supposedly involved in language control, along with the left prefrontal cortex and the supramarginal gyrus (Abutalebi and Green 2007).

Although the difference in paradigms makes it difficult to compare our study with others, it is worth emphasizing that some tasks, such as language switching and translation, engaged selectively one or two components of this control circuitry. For instance, Price et al. (1999) showed that translation (compared with reading) activated the ACC and basal ganglia (putamen and head of the caudate), whereas language switching increased activity in the inferior frontal gyrus (BA 44) and the bilateral supramarginal gyrus. Lehtonen et al. (2005) found that translation relative to control showed activation in the left inferior frontal gyrus (BA 47) and the left basal ganglia (the lateral globus pallidus). In a naming task, Hernandez et al. (2001) showed that introducing switching between languages increased activity in the right prefrontal cortex (BA 46). Rodriguez-Fornells et al. (2005) used a go/nogo covert naming task in a highly mixed bilingual context and showed that, in order to control the interference from the nontarget language, the subjects activated the left middle prefrontal cortex (BA 9/46) and the SMA. Other findings were found by studies employing the adaptation paradigm (see for definition Chee 2006). In these paradigms, similar stimuli such as words belonging to the same language are contrasted to stimuli belonging to two different languages. For instance, Chee et al. (2003) studied word repetition within and across languages and found that the “across language” condition entailed more extended left prefrontal activity (see also Klein et al. 2006 for similar findings). In another adaptation paradigm, Crinion et al. (2006) reported that left caudate activity was sensitive to changes in the language but not to a within-language condition.

Our analysis demonstrated that this language control circuitry is modulated by the situational (bilingual versus monolingual) context in which the bilinguals are placed. Concerning more specifically the caudate nucleus, Friederici (2006) has recently suggested that the left caudate might be activated when the language processing system cannot rely entirely on automatic mechanisms, but has to recruit controlled processes as well. If, as previously proposed, such a cognitive mechanism might be more required during word production in the weaker L2 to prevent unwanted prepotent interferences from the dominant language (L1), then all the areas (or some) specifically engaged during the selection of L1 (namely ACC and the caudate) should also be engaged when selecting L2 as discussed below.

Lexical Competition during the Selection of the Nondominant Language

We hypothesized that the direct comparison of L2 versus L1 naming in the LSc might induce similar activations in these areas involved in the selection of L1 names. Interestingly, we

observed that the extension of the activity in some of these structures (in particular the cingulate cortex but also inferior frontal gyrus) was greater when selecting L2 lexical items in comparison with L1 ones. Concerning the left ACC, it is worth noting that the activation observed in this comparison was much more extensive than in the other comparisons (L1 naming in LSc vs. SNC and LSc vs. TSc). The activation of the ACC has repeatedly been found in tasks implying conflict and interference monitoring (e.g., as in the Stroop task), response evaluation, and error detection such as for example when a response tendency has to be overcome as is the case for L1 names (Carter et al. 2000; Rodriguez-Fornells et al. 2005). The extended engagement of the ACC together with the greater activation in the left caudate and left inferior frontal gyrus might thus be explained in terms of differing processing demands that take place when using the nondominant language (L2). In line with the observation that second language processing is more demanding than native language processing (see for review, Perani and Abutalebi 2005), our findings suggest that selecting lexical items in the nondominant language is mediated by more controlled processing resources. The dominant language, on the other hand, seems to be processed through more automatic processing resources and may hence be less dependent on such mechanisms. Accordingly, one can predict that an increase in L2 proficiency may reduce activation in these regions associated with response control due to a much more automatic access to L2 items (French and Jacquet 2004), and consequently would diminish the between-languages competition.

Conclusions

In the present study we have shown that bilinguals might rely on a control mechanism when performing a lexical selection in a highly mixed bilingual context. Our results indicate that brain areas, which control the appropriate selection of one target language, are different from those allowing the selection between two linguistic registers within the same dominant language. Unlike the evidence gained by the study of bilingual aphasia where distinct brain areas have often been thought to be solely responsible for language switching/selection difficulties and hence for language control, functional neuroimaging allows us to disentangle the various modules of the neural network linked to language control. Language control is intimately linked to cognitive control in general, which is a complex cognitive function that should be thought in terms of dynamic interactions between separable neural systems (Gruber and Goschke 2004) including language, memory, and attentional processes. Among the various functional components that could be included in cognitive control mechanisms is the brain's ability to filter out irrelevant informations and inhibit inappropriate response tendencies (see Bunge et al. 2002). Functional studies indicate that the various subcomponents of cognitive control imply separable neural modules (Botvinick et al. 1999; Carter et al. 1998, 2000; Petrides et al. 1993) that include the prefrontal, parietal, and anterior cingulate cortex (Braver et al. 2001; Bunge et al. 2002; de Zubicaray et al. 2000) but also the basal ganglia (Graybiel 1997; Middleton and Strick 2000) thanks to its connections with the frontal, motor, and temporo-parietal cortex (Friederici 2006).

These results indicate that the left caudate nucleus and the left anterior cingulate cortex participate in the neural network

involved in between-languages selection processes in the bilingual brain. Although at this stage, the involvement of the left prefrontal cortex in this network could not be definitely ruled out, our observations indicate that this area might be more involved in within-language selection processes. Finally, our analysis showed that the recruitment of brain structures involved in language selection is even more important when the subjects are using a weaker L2.

Notes

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References

- Abutalebi J, Green D. 2007. Bilingual language production: the neurocognition of language representation and control. *J Neuro-linguistics*. 20:242-275.
- Abutalebi J, Keim R, Brambati SM, Tettamanti M, Cappa SF, De Bleser R, Perani D. 2007. Late acquisition of literacy in a native language. *Hum Brain Mapp*. 28:19-33.
- Abutalebi J, Miozzo A, Cappa S. 2000. Do subcortical structures control language selection in bilinguals? Evidence from pathological language mixing. *Neurocase*. 6:101-106.
- Aglioti S, Fabbro F. 1993. Paradoxical selective recovery in a bilingual aphasic following subcortical lesion. *NeuroReport*. 4:1359-1362.
- Alario FX, Ferrand L. 1999. A set of 400 pictures standardized for French: norms for name agreement, image agreement, familiarity, visual complexity, image variability, and age of acquisition. *Behav Res Methods Instrum Comput*. 31:531-552.
- Bookheimer S. 2002. Functional MRI of language: new approaches to understanding the cortical organization of semantic processing. *Annu Rev Neurosci*. 25:151-188.
- Botvinick M, Nystrom LE, Fissell K, Carter CS, Cohen JD. 1999. Conflict monitoring versus selection-for-action in anterior cingulate cortex. *Nature*. 402:179-181.
- Brass M, Ullsperger M, Knoesche TR, von Cramon DY, Phillips NA. 2005. Who comes first? The role of the prefrontal and parietal cortex in cognitive control. *J Cogn Neurosci*. 17:1367-1375.
- Braver TS, Barch DM. 2006. Extracting core components of cognitive control. *Trends Cogn Sci*. 10:529-532.
- Braver TS, Barch DM, Gray JR, Molfese DL, Snyder A. 2001. Anterior cingulate cortex and response conflict: effects of frequency, inhibition and errors. *Cereb Cortex*. 11:825-836.
- Bunge SA, Dudukovic NM, Thomason ME, Vaidya CJ, Gabrieli JD. 2002. Immature frontal lobe contributions to cognitive control in children: evidence from fMRI. *Neuron*. 33:301-311.
- Bush G, Luu P, Posner MI. 2000. Cognitive and emotional influences in anterior cingulate cortex. *Trends Cogn Sci*. 4:215-222.
- Cabeza R, Nyberg L. 1997. Imaging cognition: an empirical review of PET studies with normal subjects. *J Cogn Neurosci*. 9:1-27.
- Carter CS, Braver TS, Barch DM, Botvinick MM, Noll D, Cohen JD. 1998. Anterior cingulate cortex, error detection, and the online monitoring of performance. *Science*. 280:747-749.
- Carter CS, Macdonald AM, Botvinick M, Ross LL, Stenger VA, Noll D, Cohen JD. 2000. Parsing executive processes: strategic vs. evaluative functions of the anterior cingulate cortex. *Proc Natl Acad Sci USA*. 97:1944-1948.
- Casey BJ, Durston S, Fossella JA. 2001. Evidence for a mechanistic model of cognitive control. *Clin Neurosci Res*. 1:267-282.
- Chee MW. 2006. Dissociating language and word meaning in the bilingual brain. *Trends Cogn Sci*. 10:527-529.
- Chee MW, Soon CS, Lee HL. 2003. Common and segregated neuronal networks for different languages revealed using functional magnetic resonance adaptation. *J Cogn Neurosci*. 15:85-97.
- Christoffels IK, Formisano E, Schiller NO. 2007. Neural correlates of verbal feedback processing: an fMRI study employing overt speech. *Hum Brain Mapp*. 28:868-879.
- Colomé A. 2001. Lexical activation in bilinguals' speech production: language-specific or language independent? *J Mem Lang*. 45:721-736.
- Content A, Mousty P, Radeau M. 1990. Bruelex: Une base de données lexicales informatisée pour le français écrit et parlé. *Annee Psychol*. 90:551-566.
- Costa A, Caramazza A. 1999. Is lexical selection in bilinguals language-specific? Further evidence from Spanish-English bilinguals and English-Spanish bilinguals. *Biling Lang Cogn*. 2:231-244.
- Crinion J, Turner R, Grogan A, Hanakawa T, Noppeney U, Devlin JT, Aso T, Urayama S, Fukuyama H, Stockton K, et al. 2006. Language control in the bilingual brain. *Science*. 312:1537-1540.
- Cycowicz YM, Friedman D, Rothstein M, Snodgrass JG. 1997. Picture naming by young children: norms for name agreement, familiarity, and visual complexity. *J Exp Child Psychol*. 65:171-237.
- De Bot K, Schreuder R. 1993. Word production and the bilingual lexicon. In: Schreuder R, Weltens B, editors. *The bilingual lexicon*. Amsterdam/Philadelphia: John Benjamins. p. 191-214.
- De Groot A, Kroll J, editors. 1997. *Tutorials in bilingualism: psycholinguistic perspectives*. New York: Lawrence Erlbaum Associates.
- de Zubicaray GI, Zelaya FO, Andrew C, Williams SC, Bullmore ET, Dumanoir C. 2000. Cerebral regions associated with verbal response initiation, suppression and strategy use. *Neuropsychologia*. 38:1292-1304.
- D'Esposito M, Detre JA, Alsop DC, Shin RK, Atlas S, Grossman M. 1995. The neural basis of the central executive system of working memory. *Nature*. 378:279-281.
- Donaldson DI, Buckner RL. 2001. Effective paradigm design. In: Matthews PM, Jezzard P, Evans AC, editors. *Functional magnetic resonance imaging of the brain: methods for neuroscience*. Oxford: Oxford University Press. p. 175-195.
- Dosenbach NU, Visscher KM, Palmer ED, Miezin FM, Wenger KK, Kang HC, Burgund ED, Grimes AL, Schlaggar BL, Petersen SE. 2006. A core system for the implementation of task sets. *Neuron*. 50:799-812.
- Dreher JC, Koechlin E, Ali SO, Grafman J. 2002. The roles of timing and task order during task switching. *NeuroImage*. 17:95-109.
- Ellis AW, Burani C, Izura C, Bromiley A, Venneri A. 2006. Traces of vocabulary acquisition in the brain: evidence from covert object naming. *NeuroImage*. 33:958-968.
- Fabbro F, Peru A, Skrap M. 1997. Language disorders in bilingual patients after thalamic lesions. *J Neurolinguistics*. 10:347-367.
- Fabbro F, Skrap M, Aglioti S. 2000. Pathological switching between languages after frontal lesions in a bilingual patient. *J Neurol Neurosurg Psychiatry*. 68:650-652.
- Francis WS. 1999. Cognitive integration of language and memory in bilinguals: semantic representation. *Psychol Bull*. 125:193-222.
- French RM, Jacquet M. 2004. Understanding bilingual memory: models and data. *Trends Cogn Sci*. 8:87-93.
- Friederici AD. 2002. Towards a neural basis of auditory sentence processing. *Trends Cogn Sci*. 6:78-84.
- Friederici AD. 2006. What's in control of language? *Nat Neurosci*. 9:991-992.
- Friston KJ, Holmes AP, Price CJ, Buchel C, Worsley KJ. 1999. Multisubject fMRI studies and conjunction analyses. *NeuroImage*. 10:385-396.
- Friston KJ, Williams S, Howard R, Frackowiak RS, Turner R. 1996. Movement-related effects in fMRI time-series. *Magn Reson Med*. 35:346-355.
- Gabrieli JD, Poldrack RA, Desmond JE. 1998. The role of the left prefrontal cortex in language and memory. *Proc Natl Acad Sci USA*. 95:906-913.
- Genzel G, Kerkhoff G, Scheffter S. 1995. PC-gestuetzte Standardisierung des Bildmaterials von Snodgrass & Vanderwart (1980). *Neurolinguistik*. 9:41-53.

- Gollan T, Kroll J. 2001. Lexical access in bilinguals. In: Rapp B, editor. A handbook of cognitive neuropsychology: what deficits reveal about the human mind. New York: Psychology Press. p. 321-345.
- Grainger J. 1993. Visual word recognition in bilinguals. In: Schreuder R, Weltens B, editors. The bilingual lexicon. Amsterdam/Philadelphia: John Benjamins. p. 11-25.
- Grainger J, Dijkstra A. 1992. On the representation and use of language information in bilinguals. In: Harris RJ, editor. Cognitive processing in bilinguals. Amsterdam: Elsevier. p. 207-220.
- Graybiel AM. 1997. The basal ganglia and cognitive pattern generators. *Schizophr Bull.* 23:459-469.
- Green D. 1986. Control, activation, and resource: a framework and a model for the control of speech in bilinguals. *Brain Lang.* 27:210-223.
- Green DW. 1998. Mental control of the bilingual lexico-semantic system. *Biling Lang Cogn.* 1:67-81.
- Grosjean F. 1992. Another view of bilingualism. In: Harris RJ, editor. Cognitive processing in bilinguals. Amsterdam: Elsevier. p. 51-62.
- Grosjean F. 2001. The bilingual's language modes. In: Janet L, editor. One mind, two languages: bilingual sentence processing. Oxford: Blackwell. p. 1-22.
- Gruber O, Goschke T. 2004. Executive control emerging from dynamic interactions between brain systems mediating language, working memory and attentional processes. *Acta Psychol (Amst).* 115:105-121.
- Heim S, Amunts K, Mohlberg H, Wilms M, Friederici AD. 2006. Head motion during overt language production in functional magnetic resonance imaging. *NeuroReport.* 17:579-582.
- Hermans D, Bongaerts T, de Bot K, Schreuder R. 1999. Producing words in a foreign language: can speakers prevent interference from their first language? *Biling Lang Cogn.* 1:213-229.
- Hernandez AE, Dapretto M, Mazziotta J, Bookheimer S. 2001. Language switching and language representation in Spanish-English bilinguals: an fMRI study. *NeuroImage.* 14:510-520.
- Jackson GM, Swainson R, Cunnington R, Jackson SR. 2001. ERP Correlates of executive control during repeated language-switching. *Biling Lang Cogn.* 4:169-178.
- Johnstone T, Ores Walsh KS, Greischar LL, Alexander AL, Fox AS, Davidson RJ, Oakes TR. 2006. Motion correction and the use of motion covariates in multiple-subject fMRI analysis. *Hum Brain Mapp.* 27:779-788.
- Kapur S, Rose R, Liddle PF, Zipursky RB, Brown GM, Stuss D, Houle S, Tulving E. 1994. The role of the left prefrontal cortex in verbal processing: semantic processing or willed action? *NeuroReport.* 5:2193-2196.
- Klein D, Watkins KE, Zatorre RJ, Milner B. 2006. Word and nonword repetition in bilingual subjects: a PET study. *Hum Brain Mapp.* 27:153-161.
- Kroll JF, Bobb SC, Wodniecka Z. 2006. Language selectivity is the exception, not the rule: arguments against a fixed locus of language selection in bilingual speech. *Biling Lang Cogn.* 9:119-135.
- Kroll JF, Stewart E. 1994. Category interference in translation and picture naming: evidence for asymmetric connections between bilingual memory representations. *J Lang Mem.* 33:149-174.
- Lawrence AD. 2000. Error correction and the basal ganglia: similar computations for action, cognition and emotion? *Trends Cogn Sci.* 4:365-367.
- Lee MW, Williams JN. 2001. Lexical access in spoken word recognition by bilinguals: evidence from the semantic competitor priming paradigm. *Biling Lang Cogn.* 4:233-248.
- Lehéricy S, Cohen L, Bazin B, Samson S, Giacomini E, Rougetet R, Hertz-Pannier L, Le Bihan D, Marsault C, Baulac M. 2000. Function MR evaluation of temporal and frontal language dominance compared with the wada test. *Neurology.* 54:1625-1633.
- Lehtonen MH, Laine M, Niemi J, Thomsen T, Vorobyev VA, Hugdahl K. 2005. Brain correlates of sentence translation in Finnish-Norwegian bilinguals. *NeuroReport.* 16:607-610.
- Marien P, Abutalebi J, Engelborghs S, De Deyn PP. 2005. Pathophysiology of language switching and mixing in an early bilingual child with subcortical aphasia. *Neurocase.* 11:385-398.
- Middleton FA, Strick PL. 2000. Basal ganglia output and cognition: evidence from anatomical, behavioral, and clinical studies. *Brain Cogn.* 42:183-200.
- Nebel K, Wiese H, Stude P, de Greiff A, Diener HC, Keidel M. 2005. On the neural basis of focused and divided attention. *Brain Res Cogn Brain Res.* 25:760-776.
- Perani D, Abutalebi J. 2005. The neural basis of first and second language processing. *Curr Opin Neurobiol.* 15:202-206.
- Petrides M, Alivisatos B, Meyer E, Evans AC. 1993. Functional activation of the human frontal cortex during the performance of verbal working memory tasks. *Proc Natl Acad Sci USA.* 90:878-882.
- Price CJ, Devlin JT, Moore CJ, Morton C, Laird AR. 2005. Meta-analyses of object naming: effect of baseline. *Hum Brain Mapp.* 25:70-82.
- Price CJ, Friston KJ. 1997. Cognitive conjunction: a new approach to brain activation experiments. *NeuroImage.* 5:261-270.
- Price CJ, Green DW, von Studnitz R. 1999. A functional imaging study of translation and language switching. *Brain.* 122(Pt 12): 2221-2235.
- Rodriguez-Fornells A, van der Lugt A, Rotte M, Britti B, Heinze HJ, Munte TF. 2005. Second language interferes with word production in fluent bilinguals: brain potential and functional imaging evidence. *J Cogn Neurosci.* 17:422-433.
- Rogers R, Monsell S. 1995. Costs of a predictable switch between simple cognitive tasks. *J Exp Psychol Gen.* 124:207-231.
- Saccuman MC, Cappa SF, Bates EA, Arevalo A, Della Rosa P, Danna M, Perani D. 2006. The impact of semantic reference on word class: an fMRI study of action and object naming. *NeuroImage.* 32:1865-1878.
- Seghier ML, Lazeyras F, Pegna AJ, Annoni JM, Zimine I, Mayer E, Michel CM, Khateb A. 2004. Variability of fMRI activation during a phonological and semantic language task in healthy subjects. *Hum Brain Mapp.* 23:140-155.
- Snodgrass JG, Vanderwart M. 1980. A standardized set of 260 pictures: norms for name agreement, image agreement, familiarity and visual complexity. *J Exp Psychol.* 6:174-215.
- Swainson R, Cunnington R, Jackson GM, Rorden C, Peters AM, Morris PG, Jackson SR. 2003. Cognitive control mechanisms revealed by ERP and fMRI: evidence from repeated task-switching. *J Cogn Neurosci.* 15:785-799.
- Swainson R, Jackson SR, Jackson GM. 2006. Using advance information in dynamic cognitive control: an ERP study of task-switching. *Brain Res.* 1105:61-72.
- Talairach J, Tournoux P. 1988. Co-planar stereotaxic atlas of the human brain. New York: Thieme.
- Thompson-Schill SL, D'Esposito M, Aguirre GK, Farah MJ. 1997. Role of left inferior prefrontal cortex in retrieval of semantic knowledge: a reevaluation. *Proc Natl Acad Sci USA.* 94:14792-14797.
- Thompson-Schill SL, D'Esposito M, Kan IP. 1999. Effects of repetition and competition on activity in left prefrontal cortex during word generation. *Neuron.* 23:513-522.
- Warburton E, Wise RJ, Price CJ, Weiller C, Hadar U, Ramsay S, Frackowiak RS. 1996. Noun and verb retrieval by normal subjects. Studies with PET. *Brain.* 119(Pt 1):159-179.
- Wartenburger I, Heekeren HR, Abutalebi J, Cappa S, Villringer A, Perani D. 2003. Early setting of grammatical processing in the bilingual brain. *Neuron.* 37:159-170.