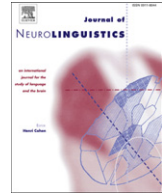




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Neural mechanisms of language switch

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ABSTRACT

Interest has continued in the neural substrates of language switch, which allows multilingual people to select an appropriate language. Using functional magnetic resonance imaging, we investigated the neural substrates for switching between different languages (cross-language switch) in comparison with those for switching between different tasks or between different action sequences. Subjects were 20 native Japanese (L1) speakers with moderate to high proficiency in English (L2). They were asked to judge pronunciation of visually presented Arabic numerals in either L1 or L2 (phonological judgment task) or the numerical meaning of the same stimuli (numerical judgment task). The switching of the tasks was semi-randomly cued by a background color change. Several brain regions showed significantly greater activity for the forward cross-language switching (L1 to L2) than the backward cross-language switching (L2 to L1). Such cross-language switch regions included the right prefrontal cortex (PFC), left superior temporal/supramarginal gyrus (STG/SMG), anterior cingulate cortex (ACC), left inferior frontal gyrus (IFG), and caudate nucleus. Among these cross-language switch regions, the left IFG and caudate nucleus were also involved in the task switching (switching between the phonological and numerical tasks). These findings were supported by an action-sequence switch experiment examining brain activity during switching

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among different tapping sequences. In the right PFC, moreover, activity during the forward cross-language switching was positively correlated with the subjects' proficiency in L2. The present study suggests that the right PFC, left IFG, left STG/SMG, ACC, and caudate nucleus might subserve differential aspects of cross-language switch in late bilinguals.

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1. Introduction

Proficient bilinguals can use their native first (L1) and learned second (L2) languages interchangeably in everyday life, and they can instantaneously select the right word from the appropriate language lexicon in a given context. A neurocognitive model proposes that bilinguals may have language-specific or “language-tagged” lexical representations sharing the same concept at the semantic level (French & Jacquet, 2004). Therefore, to select the right word, bilinguals need to activate the lexicon of the target language and simultaneously inhibit interference from the non-target language (Costa & Santesteban, 2004; Price, Green, & Von Studnitz, 1999). These processes are particularly important when bilinguals switch from one language to another, and the underlying cognitive mechanisms are called language switch or language switching (called language switch hereafter). To achieve language switch, bilinguals should possess the neural devices to effectively switch despite competition between different languages, especially considering that L1 and L2 probably have overlapping neuroanatomical bases (Crinion et al., 2006; Xue, Dong, Jin, Zhang, & Wang, 2004).

Many neuroimaging studies have already explored the neural correlates of the mechanisms that switch between different languages in bilinguals. These studies indicated that the language switch mechanisms might depend on cortical and subcortical circuits: the left caudate nucleus (Crinion et al., 2006), prefrontal cortex (PFC; Abutalebi & Green, 2007; Chee, Soon, & Lee, 2003; Hernandez, Martinez, & Kohnert, 2000; Rodriguez-Fornells et al. 2005), left inferior frontal gyrus (IFG; Kho et al., 2007; Price et al., 1999; Quaresima, Ferrari, van der Sluijs, Menssen, & Colier, 2002; Wang, Xue, Chen, Xue, & Dong, 2007), anterior cingulate cortex (ACC; Abutalebi, Annoni et al., 2007; Abutalebi, Brambati et al., 2007; Wang et al., 2007), and left temporo-parietal areas including the superior temporal gyrus (STG; Moritz-Gasser & Duffau, 2009) and supramarginal gyrus (SMG; Hernandez, Dapretto, Mazziotta, & Bookheimer, 2001; Khateb et al., 2007; Price et al., 1999; Venkatraman, Siong, Chee, & Ansari, 2006; Wang et al., 2007). Among these areas, the PFC, ACC, and the caudate nucleus are also known for their roles in executive switch, such as switching between cognitive sets (Brass, Ullsperger, Knoesche, von Cramon, & Phillips, 2005; Braver, Barch, Gray, Molfese, & Snyder, 2001; Dosenbach et al., 2006; Dove, Pollmann, Schubert, Wiggins, & von Cramon, 2000; Funahashi, 2001; Kimberg, Aguirre, & D'Esposito, 2000).

Considering those overlapping neural correlates, it seems possible to regard the language switch as a special case of behavioral switch. Here, to better understand the neural mechanisms of language switch, we examined neural activity during language switching, cognitive-task switching, and action-sequence switching conditions. We compared switching between different languages (L1 versus L2) for performing the same task (phonology judgment) and switching between different language-based tasks (phonology judgment versus numeral judgment). Because the present subject group had different proficiency/exposure levels between L1 and L2, the direction of language switch was considered to induce an asymmetry in brain activity. We hypothesized that the more demanding switch from stronger L1 to weaker L2 (forward cross-language switching) would activate the language switch areas more than the opposite (backward cross-language switching). Next, we hypothesized that the forward cross-language switch may include neural mechanisms to switch from a habitual behavior into a less solid one. In an action-sequence switch experiment, we investigated brain activity during action switching among different tapping sequences: two remembered ones and a freely generated one. Switching from a remembered sequence into a free sequence was considered to include a cognitive component when switching from a habitual action to a less experienced action, a possible

component involved in the forward language switch. Finally, we tested if activity in the cross-language switching areas was sensitive to the subject's proficiency in L2.

2. Methods

2.1. Subjects

The present study consisted of a main experiment (language and task switch) and a sequence switch experiment. Twenty native Japanese speakers (11 men and 9 women) with a mean age of 26.1 years ($SD = 5.9$, range 23–42) participated in the main experiment. The participants in the action-sequence switch experiment were 18 healthy volunteers (10 men and 8 women; mean age = 26.1 years old, $SD = 4.8$, range 20–28), and all of them participated in the main experiment. All participants were right-handed as assessed by the Edinburgh Handedness Inventory. They were healthy and neurologically intact, with no history of psychotropic medication use or head injury. The study protocol was approved by the institutional review board (National Center of Neurology and Psychiatry). All participants gave written informed consent prior to the study.

The participants were university students or graduates, all of whom had grown up in Japan. The participants started to learn English as their second language (L2) at a mean age of 11.0 years old (range = 6–13; Table 1). To quantify proficiency in English, the subjects underwent the English Vocabulary Test (EVT), the National Adult Reading Test, and the Graded Naming Test (Table 1). The participants also self-evaluated their ability in L2 for reading, writing, speaking, and listening comprehension on a 10-point scale ranging from one being “not at all skilled” to 10 being “very skilled.” The mean scores from the self-assessment scale (Table 1) indicated a fair level of proficiency in English as an L2. In addition, the participants completed a questionnaire assessing the percentage of exposure to both languages in daily life (Table 1). In summary, L2 proficiency of the present participants was somewhat variable, from moderate to high, and all participants had limited exposure to L2 in daily life.

2.2. Experimental design

2.2.1. Main experiment (language and cognitive-task switch experiment)

An event-related functional magnetic resonance imaging (fMRI) design was employed in the main experiment. The subjects underwent a single scanning run, which lasted for 14 min 7 s and included 353 task trials. For each trial, a 2-digit Arabic number stimulus was presented at the center of view with a stimulus onset asynchrony (SOA) of 2.5 s (Fig. 1a). The number ranged from thirteen to ninety-nine. Each number stimulus was displayed in white and was surrounded by a colored square (visual angle of

Table 1

Mean and standard deviation of the measures of the subject's language backgrounds, proficiency tests, and self-assessments in the main experiments.

Measure	Mean	SD
<i>Language background</i>		
Age of first exposure (years)	11.1	3.4
Duration of formal learning (years)	11.0	4.4
EVT	29.0	20.8
NART	27.8	12.7
GNT	12.8	13.9
<i>Self-assessment (scale 1–10)</i>		
Reading	7.6	1.3
Writing	6.7	1.1
Speaking	5.4	2.3
Listening Comprehension	5.7	2.4
<i>Daily exposure to each language (%)</i>		
Japanese	78.7	2.5
English	21.3	3.0

EVT, English Vocabulary Test; NART, National Adult Reading Test; GNT, Grand Naming Test; Self-assessment ranging from 1 (not at all skilled) to 10 (very skilled comparable to native speakers).

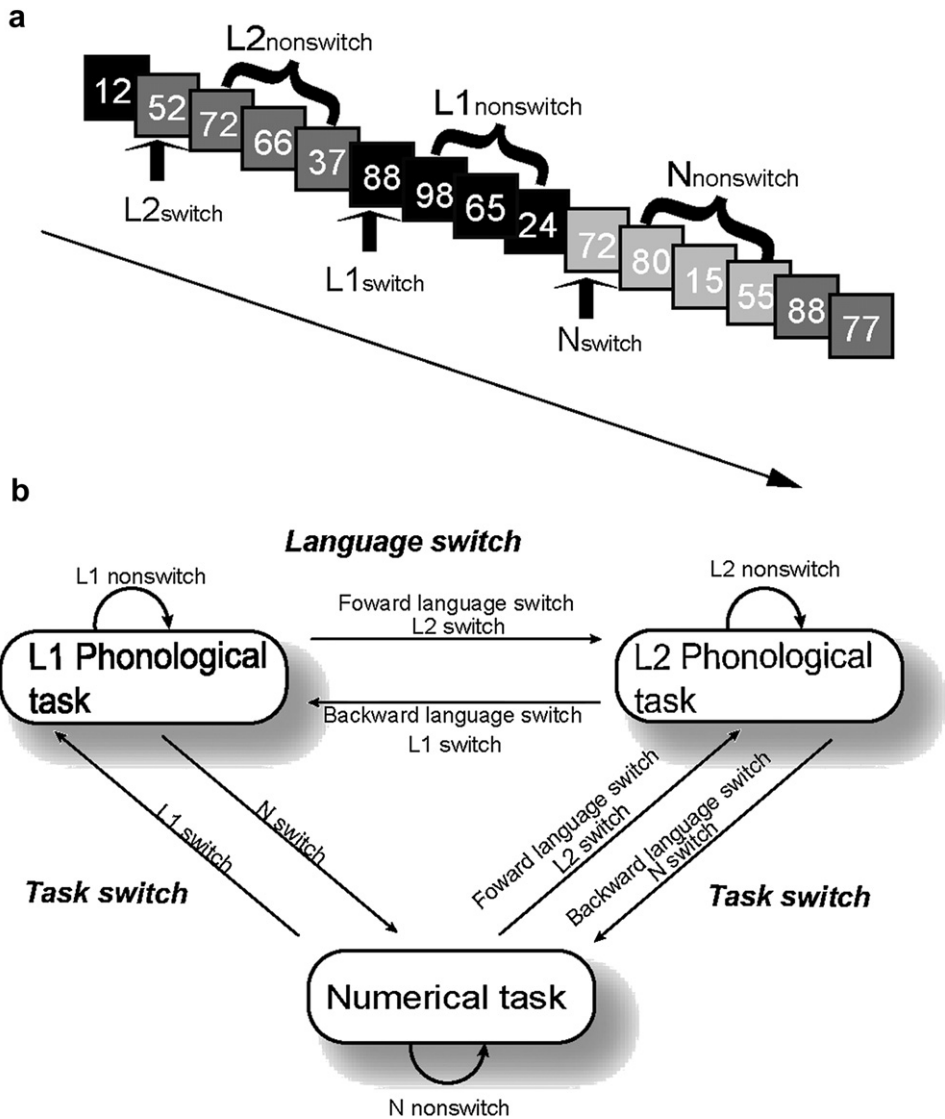


Fig. 1. (a) Scheme showing the sequence of events and stimuli in the task. For each trial, a 2-digit Arabic number stimulus was presented at the center of view (stimulus onset asynchrony of 2.5 s). Each number stimulus was surrounded by a colored square indicating the current task, and the task/language switching was informed by the change of the square color. After each color change, the background color remained the same for 4–6 stimuli, yielding several consecutive non-switching trials ($N_{\text{nonswitch}}$, $L1_{\text{non-switch}}$, and $L2_{\text{non-switch}}$). Switching types were defined as follows: $L1-N_{\text{switch}}$ (numerical task switched from L1 phonological task), $L2-N_{\text{switch}}$ (numerical task switched from L2 phonological task), $L2-L1_{\text{switch}}$ (L1 phonological task switched from L2 phonological task), $N-L1_{\text{switch}}$ (L1 phonological task switched from numerical task), $L1-L2_{\text{switch}}$ (L2 phonological task switched from L1 phonological task), and $N-L2_{\text{switch}}$ (L2 phonological task switched from numerical task). (b) A cognitive model of the experimental paradigm. Repetition of the same color stimuli yielded three types of non-switching trials ($L1_{\text{non-switch}}$, $L2_{\text{non-switch}}$, and $N_{\text{nonswitch}}$), and color switch trials gave two types of switching trials (language switch shown in black arrows, task switch shown in gray arrows). The language switch included L1-L2 phonological task switching (forward language switch) and L2-L1 phonological task switching (backward language switch).

~2.5°). The color of the square (blue, green, or red) served as a conditional stimulus and instructed the subjects to attend to one of the three attributes of the number stimuli: phonology in Japanese, phonology in English, or numerical meaning.

For the phonological judgment task in either Japanese (L1) or English (L2), the subjects were required to judge whether the number included the phoneme of [n] before a consonant or a silent vowel or at the end of the word. In this task, the subjects were instructed to read the numbers at least once covertly in the target language and to judge the pronunciation as should be described in pronunciation dictionaries in each language. In L2, this phoneme appears in numbers with one, seven, nine, seventy, ninety, and all the teens, and in L1 this appears in numbers with 'san' (3 in Japanese) and 'yon', (4), 'sanju' (30), and 'yonju' (40). In the numerical judgment task, the subjects reported whether the number stimulus was a multiple-of-three or not.

The subjects reported their judgment by pressing a button with the index finger or the middle finger of the right hand, and the response time (RT) and accuracy were recorded and analyzed. In a pilot experiment, when we employed a simpler numerical judgment task between even and odd numbers, the RT was much shorter in the even-odd judgment task than the phonological judgment tasks. The next pilot study showed that RT and accuracy were comparable between the multiple-of-three judgment and the L1/L2 phonology tasks. Hence, we decided to run the main experiment with the multiple-of-three task.

The frequency of stimulus appearance was adjusted so that the occurrence rate of the yes or no response was almost equal across the three types of tasks: (1) the numerical judgment task (N), (2) the phonological task for L1 (L1), and (3) the phonological task for L2 (L2). The task switching was informed by the change of the square color without any other warning stimuli. Two trial types (switching and non-switching trials) were defined for each task. In a scanning run, 56 switching trials were defined. The cognitive-task switch trials had four types: (1) L1-N_{switch} (i.e., the numerical task switched from the L1 phonological task), (2) L2-N_{switch}, (3) N-L1_{switch}, and (4) N-L2_{switch} (Fig. 1b). The language-switch trials included 14 switching trials each for L1-L2_{switch} (L2 switched from L1 within the phonological task) and for L2-L1_{switch} (L1 switched from L2 within the phonological task). The L1-L2_{switch} and L2-L1_{switch} corresponded to the "forward" and "backward" language switch, respectively. After each color change, the background color remained the same for 4–6 stimuli, yielding three types of non-switching trials (N_{non-switch}, L1_{non-switch} and L2_{non-switch}). Thus, 4–6 non-switching trials always followed each switching trial, and the switching trials were presented every 12.5 s on average. There were 356 non-switching trials in total. In addition, a baseline condition (12.5-s duration) was semi-randomly inserted in a scanning run. In the baseline blocks, the participants were only asked to look at two zeros displayed abreast in white within a gray square with an SOA of 2.5 s (35 trials in total).

In the present study, instruction cues (colored squares) were presented together with the number stimuli, so that the timing of switching was clearly determined without using extra warning stimuli. Furthermore, the use of Arabic numbers should have helped to eliminate visual images related to recognition of picture stimuli, while still allowing for language-specific phonological responses to the same stimuli.

2.2.2. Action-sequence switch experiment

To check the involvement of the language switch areas in switching between habitual and less-habitual behaviors, the action-sequence switch experiment investigated brain activity during switching between different sequences. The subjects underwent a single scanning run (14 min 7 s), which required the generation of two types of remembered tapping sequences and that of free tapping sequences. The remembered sequence conditions involved serial button pressing with a sequence of 1-3-2-3-2-1 (Seq1) or 1-1-2-3-3-3 (Seq2), where the numbers 1, 2, and 3 indicated the index, middle, and ring fingers of the right hand, respectively. In the free sequence condition (SeqF), the participants were required to generate a new sequence consisting of six taps involving the index, middle, and ring fingers freely.

Similar to the language switch experiment, each condition was instructed by a colored square (red, blue, and green) presented at the center of view with SOA of 2.5 s. The same colored square was presented repeatedly for 4–6 stimuli, yielding non-switching trials (Seq1_{non-switch}, Seq2_{non-switch}, and SeqF_{non-switch}). During the task period, the participants were instructed to keep tapping response buttons 6 times within 2.5 s (~2.4Hz tapping frequency) following the color–sequence association

rule. The colored square was changed every 12.5 s on average, yielding trials that involved switching between the conditions of sequence generation (Seq_{1switch}, Seq_{2switch}, and Seq_{Fswitch}). For the baseline condition, the subjects were only asked to look at a gray square presented for 12.5 s. The participants were familiarized with the two remembered sequences as well as an association rule between the colors and the task conditions prior to the experiment. Before each experiment, the subjects were allowed to practice the task until they learned the rules and the two sequences perfectly and responded correctly in over 90% of the trials. This procedure assured that the Seq₁ and Seq₂ conditions were well-trained habitual actions.

2.3. Data acquisition

In both experiments, functional imaging data were obtained on a 3-T magnetic resonance imaging (MRI) scanner (Siemens Trio, Erlangen, Germany) with an 8-channel phased array receiver-only coil. The subject lay supine on the scanner bed, wore MRI-compatible goggles (Resonance Technology, Burbank, CA, USA), and held a button-response unit (Current Designs, Philadelphia, PA, USA) with their right hand. The visual stimuli were delivered through the goggles. The stimulus presentation was switch by Presentation software (Neurobehavioral Systems, Albany, CA, USA) on a personal computer and was synchronized with the trigger pulses from the scanner. For functional images in both experiments, a gradient-echo, echo-planar imaging (EPI) sequence was used to acquire 44 interleaved axial slices covering the whole brain as follows: repetition time (TR) = 3000 ms, echo time (TE) = 30 ms, flip angle (FA) = 90°, slice thickness = 3 mm without interslice gaps, matrix size = 64 × 64, field of view (FOV) = 192 mm. For each subject, the first two volumes in each scan series were not saved because they were collected before magnetization reached the equilibrium state. High-resolution, three-dimensional T1-weighted anatomical images were obtained with magnetization-prepared rapid gradient-echo images (TR = 2000 ms, TE = 4.4 ms, FA = 80°, slice thickness = 1 mm, matrix size = 192 × 176, FOV = 192 × 176 mm).

2.4. Behavioral data analysis

The accuracy and RT were recorded and analyzed. The data from the main experiment were analyzed by a repeated-measures analysis of variance (RM-ANOVA) with the task type (L1, L2, and N) and the trial type (switching and non-switching) as within-subject variables. That is, in this categorical analysis, the N_{switch} included L1-N_{switch} and L2-N_{switch}; the L1_{switch} included N-L1_{switch} and L2-L1_{switch}; and the L2_{switch} included L1-L2_{switch} and N-L2_{switch}. The forward language switch (L1-L2_{switch}) and the backward language switch (L2-L1_{switch}) conditions were separately compared with a paired *t*-test. In the action-sequence switch experiment, the RT was defined as the time interval between the stimulus presentation and the first of the serial button-press responses. The data from the action-sequence switch experiment were analyzed by an RM-ANOVA with the task type (Seq₁, Seq₂, and Seq_F) and the trial type (switching and non-switching) as within-subject variables. In this analysis, the Seq_{1switch} included Seq₂-Seq_{1switch} and Seq_F-Seq_{1switch}; the Seq_{2switch} included Seq₁-Seq_{2switch} and Seq_F-Seq_{2switch}; and the Seq_{Fswitch} included Seq₁-Seq_{Fswitch} and Seq₂-Seq_{Fswitch}. Additionally, assuming that the Seq₁ and Seq₂ became well-trained habitual actions during the training period, we defined the Seq₁-Seq_{Fswitch} and Seq₂-Seq_{Fswitch} to be “forward habitual-action switch” and the Seq_F-Seq_{1switch} Seq_F-Seq_{2switch} to be “backward habitual-action switch.” The data from the forward and the backward habitual-action switch conditions were compared with a paired *t*-test. Finally, the cost of the forward cross-language switching (i.e., difference in RTs between L1-L2_{switch} and L2_{non-switch}) was compared with that of the forward action switching (difference in RTs between Seq₁-Seq_{Fswitch}/Seq₂-Seq_{Fswitch} and Seq_F_{nonswitch}) using a *t*-test.

2.5. Imaging analysis

All pre-processing steps and statistical analyses were performed with SPM5 (<http://www.fil.ion.ucl.ac.uk/spm>; Wellcome Department of Cognitive Neurology, London, UK) on Matlab 6.5 (Mathworks, Natick, MA, USA). A slice-timing procedure was applied to correct for differences in acquisition timing at the slice level. The functional volumes were then spatially realigned to the first EPI volume. The

realigned images were spatially normalized to fit into the EPI template defined in the Montreal Neurological Institute stereotactic space. Finally, all normalized images were spatially smoothed with a Gaussian kernel of 8-mm full-width at half-maximum.

The effects of the task components were assessed on a voxel-by-voxel basis using the general linear model. The final statistical parametric maps for inference were generated using a random effects model (Friston, Holmes, Price, Büchel, & Worsley, 1999) as achieved with a standard two-stage procedure. At the first level, a design matrix incorporating task/trial effects and effects of no interest was built for each individual subject. Regressors modeling trial events were convolved with a canonical hemodynamic response function along with its first-order time derivative. Six regressors summarizing head motion estimated during the realignment procedure were also included in the design matrix. Parameter estimates for the regressors were obtained by restricted maximum-likelihood estimation. By applying appropriate linear contrasts, the first-level analysis yielded summary images representing the effects of interest. These summary images were fed into the second-level analysis. At the second-level, group analyses based on the random effects model were conducted to generalize statistical inference obtained from our sample to the population. Statistical parametric maps (SPMs) for the task effects were generated by one-sample *t*-tests for each condition.

2.5.1. Main experiment

The following SPMs were obtained from the second-level analysis by considering three levels (N, L1, and L2) in the task category and two levels (switching and non-switching) in the trial category. However, to make interpretation of the results simple, the comparison between these experimental factors was divided into two parts. In the first part, we concentrated on analyzing the task and trial effects within the phonological task, especially paying attention to the effects of the language switch. First, the main effects of switching, i.e., ($L1-L2_{\text{switch}}$ & $L2-L1_{\text{switch}}$) versus non-switching ($L1_{\text{non-switch}}$ & $L2_{\text{non-switch}}$), were examined (Effect 1: Cross-language switching). Second, the main effects of the language used were considered as follows: ($L2-L1_{\text{switch}}$ & $L1_{\text{non-switch}}$) versus ($L1-L2_{\text{switch}}$ & $L2_{\text{non-switch}}$) (Effect 2: Language). Third, the effects of forward and backward cross-language switching were separately defined as follows: $L1-L2_{\text{switch}}$ minus $L2_{\text{non-switch}}$ (Effect 3: Forward cross-language switching) and $L2-L1_{\text{switch}}$ minus $L1_{\text{non-switch}}$ (Effect 4: Backward cross-language switching). Finally, the interaction between the switching and language components was considered to detect activity depending on the direction of language switch with the contrast of ($L1-L2_{\text{switch}}$ minus $L2_{\text{non-switch}}$) versus ($L2-L1_{\text{switch}}$ minus $L1_{\text{non-switch}}$). We had a specific a priori hypothesis that switching from L1 to L2 would more strongly activate the language switch areas than the opposite in the present participants who had asymmetry in language proficiency. Therefore, we were especially interested in the contrast of ($L1-L2_{\text{switch}}$ minus $L2_{\text{non-switch}}$) minus ($L2-L1_{\text{switch}}$ minus $L1_{\text{non-switch}}$), which should depict the neural substrates for the forward cross-language switching after a general component for cross-language switching was controlled (Effect 5: Forward versus backward cross-language switching).

In the second part, we examined the effects of cognitive-task switching between the numerical and phonological tasks. First, the main effects of cognitive-task switching, i.e., ($L1-N_{\text{switch}}$ & $L2-N_{\text{switch}}$ & $N-L1_{\text{switch}}$ & $N-L2_{\text{switch}}$) versus non-switching ($L1_{\text{non-switch}}$ & $L2_{\text{non-switch}}$ & $N_{\text{non-switch}}$), were considered (Effect 6: Task switching). Second, although the semantic meaning of numerals was regarded as language neutral (Macnamara, Krauthammer, & Bolgar, 1968; Meuter & Allan, 1999), it was unclear whether the numerical judgment task accompanied phonological processes in either L1 or L2 in the current subject group. We hence checked whether the task switch effect was asymmetric when the language in the phonological task before or after the numerical judgment differed: ($L2-N_{\text{switch}}$ & $N-L2_{\text{switch}}$) versus ($L1-N_{\text{switch}}$ & $N-L1_{\text{switch}}$) (Effect 7: Language-sensitive task switching).

In all the analyses, statistical inference was based on a spatial extent threshold of $p < 0.05$ family-wise error (FWE) corrected for multiple comparisons after a height threshold was set at $p < 0.001$ uncorrected.

2.5.2. Action-sequence switch experiment

The following SPMs were created from the second-level analysis by considering three levels (Seq1, Seq2, and SeqF) in the sequence category and two levels (switching and non-switching) in the trial category. First, the main effects of action switching, ($\text{Seq1}_{\text{switch}}$ & $\text{Seq2}_{\text{switch}}$ & $\text{SeqF}_{\text{switch}}$) minus

(Seq1_{non-switch} & Seq2_{non-switch} & SeqF_{nonswitch}), were examined (Effect 8: Action switching). Hereafter, we concentrated on describing brain activity for switching from a well-trained tapping sequence to a new tapping sequence (Seq1-SeqF_{switch} & Seq2-SeqF_{switch}) versus non-switching (SeqF_{nonswitch}). This effect (Effect 9: Forward action switching) was considered to include a behavioral component to switch from habitual actions into a less solid action, and a similar behavioral component might be involved in switching from an experienced language into a weaker language. Activity for switching from a new sequence to a well-learned sequence, (SeqF-Seq1_{switch} & SeqF-Seq1_{switch}) versus non-switching (Seq1_{non-switch} & Seq2_{non-switch}), was also considered (Effect 10: Backward action switching). Next, we considered the effects of switching from a habitual sequence to a new sequence after controlling a general switching-related component: [(Seq1-SeqF_{switch} minus SeqF_{nonswitch}) & (Seq2-SeqF_{switch} minus SeqF_{nonswitch})] versus [(SeqF-Seq1_{switch} minus Seq1_{non-switch}) & (SeqF-Seq2_{switch} minus Seq2_{non-switch})] (Effect 11: Forward versus backward action switching). Finally, to clarify the involvement of the forward cross-language switch areas in a non-language behavioral switching, we specifically compared brain activity between the forward cross-language switch condition and the forward habitual-action switch condition as follows: (L1-L2_{switch} minus L2_{non-switch}) versus (Seq1-SeqF_{switch} minus SeqF_{non-switch}) or (Seq2-SeqF_{switch} minus SeqF_{nonswitch}). The comparison of activity for the forward language switch with activity for either the Seq1-SeqF_{switch} or the Seq2-SeqF_{switch} showed almost the same results. Therefore, we presented the results after pooling the data from the Seq1-SeqF_{switch} and the Seq2-SeqF_{switch} conditions as the SeqF_{switch} condition (Effect 12: Forward cross-language versus action switching). In this particular analysis, to avoid the influence of deactivation during the forward action switching condition, an image created from the deactivation in the forward action switch condition (Effect 9, $P < 0.05$ uncorrected) was used as an exclusion mask. Statistical inference was based on a spatial extent threshold of $p < 0.05$ (FWE-corrected) with a height threshold of $p < 0.001$ (uncorrected).

2.5.3. Small volume correction analysis

In the regions where we had an a priori hypothesis about the cross-language effects, we performed a small volume correction (SVC) analysis. We have previously shown that the left caudate nucleus plays a role in language switching (Crinion et al., 2006). For the SVC analysis, a volume-of-interest (VOI) with a 5-mm radius sphere was set up by employing a coordinate of caudate nucleus activity ($x, y, z = -8, 12, 6$) reported in the previous study (Crinion et al., 2006). Similarly, we performed an SVC analysis by placing a 5-mm radius sphere VOI at the coordinates of left STG ($x, y, z = -50, -38, 22$; Hernandez et al. 2009), and left SMG ($x, y, z = -40, -46, 40$; Price et al., 1999). Statistical inference was based on a height threshold of $p < 0.05$ corrected for the multiple comparisons within the search volume.

2.5.4. Correlation of brain activity with L2 proficiency

Finally, a voxel-wise correlation analysis was performed on the effect size images of the “forward cross-language switching” contrast (Effect 3) by using the EVT score as an explanatory variable. The EVT was employed as a representative measure of L2 fluency because it was presumed to reflect the subjects’ proficiency most accurately among the behavioral measures. The EVT, designed originally for evaluating highly proficient English learners such as students at University of Cambridge, does not contain any words from the high-frequency word category. These features were expected to induce well-behaving variability of the score reflecting L2 proficiency, which was prerequisite for the correlation-type analysis. To check the effects of L2 proficiency on behaviors during fMRI, a correlation of RT with the EVT scores was also tested. We also checked if other switching-related activities were correlated with the EVT scores.

3. Results

3.1. Behavioral data

3.1.1. Main experiment

The accuracy of responses was 98.9% (standard deviation = 2.1) in N_{nonswitch}, 97.6% (SD = 6.3) in N_{switch}, 98.9% (SD = 2.1) in L1_{non-switch}, 97.3% (SD = 5.9) in L1_{switch}, 98.2% (SD = 2.7) in L2_{non-switch}, 96.7%

(SD = 6.0), and 96.6% (SD = 6.0) in L2_{switch}. The categorical comparison of the accuracy data did not reach statistical significance for either the main effects of the task type (L1, L2, and N) [$F_{(1,19)} = 1.72$, $p = 0.95$] or the trial type (switch and non-switch) [$F_{(1,19)} = 1.98$, $p = 0.16$] or for the task-by-trial interactions [$F_{(1,19)} = 1.72$, $p = 0.95$]. The RT data were analyzed in a similar fashion. Although an RM-ANOVA failed to reveal significant main effects for the task type (L1, L2, and N) [$F_{(1,19)} = 4.70$, $p = 0.10$], the main effects for the trial type (switching and non-switching) were significant [$F_{(1,19)} = 11.42$, $p < 0.001$]. There was no significant task-by-trial interaction [$F_{(1,19)} = 1.95$, $p = 0.15$]. These results indicated that the RT of the switching trials was longer than that of the non-switching trials, but the effects of switching did not differ across the task conditions. When the RT was compared between the forward (L1-L2_{switch}) and the backward (L2-L1_{switch}) language switch conditions, no significant difference was found ($t = 1.50$, $p = 0.88$) (Fig. 2b).

3.1.2. Action-sequence switch experiment

The accuracy of responses was 97.5% (SD = 5.6) in Seq1_{switch}, 96.6% (SD = 6.1) in Seq2_{switch}, 99.0% (SD = 2.5) in Seq1_{non-switch}, and 98.5% (SD = 2.0) in Seq2_{non-switch}. The statistical analysis on RT (Fig. 2c) did not reveal significant main effects of the task type (Seq1, Seq2 and SeqF) [$F_{(1,17)} = 1.32$, $p = 0.27$], but significant main effects were found for the trial type (switching versus non-switching) [$F_{(1,17)} = 15.5$, $p < 0.001$]. A trend was found for task-by-trial interaction [$F_{(1,17)} = 2.51$, $p = 0.08$]. These results indicated that the RT of the switching trials was longer than that of the non-switching trials, but the effects of switching did not significantly differ across the sequence conditions. When the RT was compared between the forward (Seq1-SeqF_{switch} and Seq2-SeqF_{switch}) and backward (SeqF-Seq1_{switch} and SeqF-Seq2_{switch}) habitual-action switch conditions (Fig. 2d), no significant difference was found ($t = 1.27$, $p = 0.93$). Finally, a t-test failed to reveal a significant difference in RT between the switching cost for the forward cross-language switch and that for the forward habitual-action switch ($t = -0.57$, $p = 0.56$). This finding meant that the cognitive loads of switching, possibly involving habitual behavior, did not differ between the two forward switching conditions.

3.2. Neuroimaging results

3.2.1. Main experiment

The main effects of language switching within the phonological judgment (Effect 1) showed increased activation in the left inferior parietal lobe, right SMA, right inferior occipital lobe, ACC, left middle frontal gyrus, and left IFG. The main effects of the language used (Effect 2) failed to reveal significant brain activity.

We then focused on analyzing the effects of the direction of language switch on brain activity, presumably induced by asymmetry of language proficiency in the present study group. The forward cross-language switching contrast (Effect 3) revealed activity in the bilateral occipital lobe, left IFG, left STG/SMG, left inferior parietal lobe, ACC, and right PFC (Table 2a). The effects of backward cross-language switching (Effect 4) activated the bilateral occipital lobe, left IFG, left inferior parietal lobe, and ACC (Table 2b). The forward versus backward cross-language switching (Effect 5) showed significant activation in the right PFC, ACC, left IFG and left temporo-parietal regions including the STG/SMG (Fig. 3a, Table 2c). With the SVC analysis, the effect was also found in the left caudate nucleus ($x, y, z = -8, 12, 6$; $z = 3.59$, $p = 0.009$, FWE-corrected within the search volume) but not in the right caudate nucleus ($x, y, z = 8, 12, 6$; $z = 1.92$, $p = 0.09$ FWE-corrected). Conversely, the backward cross-language switching induced no extra activation relative to the forward cross-language switching.

Next, we analyzed the effects of the task switching (Effect 6), which showed significantly increased activation in the left IFG, left middle frontal gyrus (dorsal premotor area), left inferior parietal lobe, and right inferior occipital lobe (Fig. 3b, Table 3). The peak of the left IFG activity reported in the forward versus backward cross-language switching (Effect 5) seemed to be located in the ventral region ($x, y, z = -44, 4, 34$), while that reported in the task switching (Effect 6) was in the dorsal region ($x, y, z = -50, 10, 20$). However, the forward cross-language switching and task switching induced activity in both ventral and dorsal IFG regions to a similar degree. In the SVC analysis, the left caudate nucleus showed the task switching effects ($x, y, z = -8, 12, 12$; $z = 3.48$, $p = 0.01$ FWE-corrected), but the right caudate

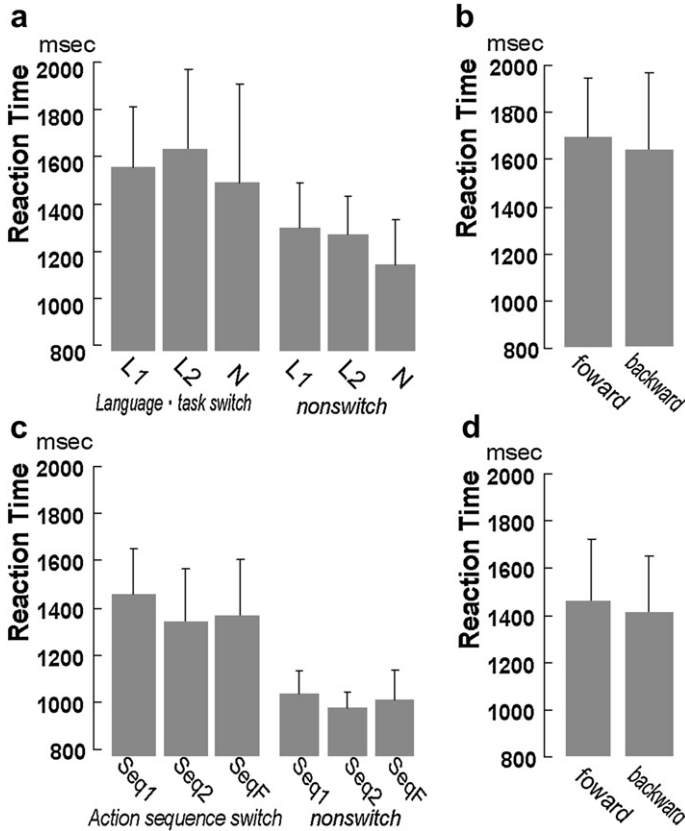


Fig. 2. (a) Reaction times (RTs) for the switching trials of the L1 phonology, L2 phonology, and numerical judgment (N) tasks and for the non-switching trials of the three tasks. The main effects for the trial type were significant as revealed by a repeated-measures analysis of variance. RTs were longer for the switching trials than the non-switching trials. The main effects of the tasks or the task-by-trial interactions were not significant. (b) RTs for the forward language switch and the backward language switch. No significant difference in RT was found (paired *t*-test). (c) RTs for the switching trials of the action switch tasks (Seq1, Seq2, and SeqF) and for the non-switching trials of the three sequence tasks. RTs were significantly longer for the switching trials than the non-switching trials, but the main effects of the tasks or the task-by-trial interactions were not significant. (d) The comparison of RTs between the forward habitual-action switch and backward habitual-action switch. No significant difference in RT was found (paired *t*-test).

nucleus did not ($x, y, z = 8, 16, 18; z = 2.35, p = 0.14$ FWE-corrected). We failed to find the cognitive-task switching-related activity sensitive to the language used for phonological judgment (Effect 7).

Plots of task-related activity supported the involvement of the right PFC and left STG/SMG in the forward cross-language switching condition, while there was only modest activity in these areas in the other conditions (Fig. 4). Marked activity was found in the left IFG, ACC, and left caudate nucleus for the forward and backward cross-language switching as well as for the task switching conditions.

3.2.2. Action-sequence switch experiment

The effect of action switching (Effect 8) induced activation in the left IFG, ACC, and bilateral parietal lobules (Table 4a), which partially overlapped with the cross-language switching-related activity. The forward action switching effect (Effect 9) activated the left IFG, left precentral gyrus, left superior occipital lobe, ACC, and bilateral inferior parietal lobules (Table 4b), while the backward switching effect (Effect 10) activated the left IFG, left occipital lobe, ACC, and left inferior parietal lobe (Table 4c). Whereas the forward action switching seemed to induce a more widespread activity than the backward action switching, the direct comparison (Effect 11) failed to find asymmetry in action switching-related activity.

Table 2

(a) Effect 3: Activities showing significant effects of the forward language switching condition as compared with the non-switching language condition. (b) Effect 4: Activities showing significant effects of the backward language switching condition as compared with the non-switching language condition. (c) Effect 5: Activities showing significant effects of the forward cross-language condition as compared with the backward cross-language condition. The threshold was set at a height threshold of $p < 0.001$ (uncorrected) and an extent threshold of $p < 0.05$ corrected for multiple comparisons in all the above contrasts.

Anatomical location	X	Y	Z	Z-value	Cluster P corrected	K_E
<i>(a) Effect 3: Forward language switching</i>						
Left occipital gyrus	-10	-68	50	5.70	0.00	1975
Left inferior frontal gyrus	-48	15	20	5.26	0.00	524
Left inferior parietal lobe	-36	-66	-32	4.64	0.00	396
Left superior temporal gyrus	-42	-30	6	4.62	0.00	306
Right occipital gyrus	4	-68	42	5.70	0.00	1975
Right anterior cingulate cortex	5	16	30	4.20	0.00	197
Right prefrontal cortex	34	8	31	3.83	0.00	397
<i>(b) Effect 4: Backward language switching</i>						
Left inferior parietal lobe	-30	-64	64	5.77	0.00	2409
Left inferior occipital lobe	-34	-86	-6	5.57	0.00	2239
Left inferior frontal gyrus	-48	7	31	5.45	0.00	1867
Right inferior occipital lobe	4	-68	42	5.70	0.00	1975
Right anterior cingulate cortex	2	30	26	5.07	0.00	305
<i>(c) Effect 5: Forward vs. backward language switching</i>						
Left superior temporal gyrus	-58	-30	23	4.55	0.00	618
Left anterior cingulate cortex	-2	18	27	4.53	0.00	655
Left supramarginal gyrus	-48	-53	32	4.21	0.00	618
Left inferior frontal gyrus	-44	4	34	4.12	0.01	160
Right prefrontal cortex	32	14	28	4.20	0.00	330

Coordinates (x, y, z) indicate local maxima in each brain region according to the Montreal Neurological Institute template.

Here, we were interested in whether the forward cross-language switch areas in the main experiment reflected behavioral switch components more general than the cross-language switch. The analysis on the forward cross-language versus forward action switching effect (Effect 12) revealed differential activation of the right PFC (Fig. 3c, Table 5). In this exploratory whole-brain comparison, no significant activation was found in the STG/SMG. The SVC method, however, revealed the effect of the

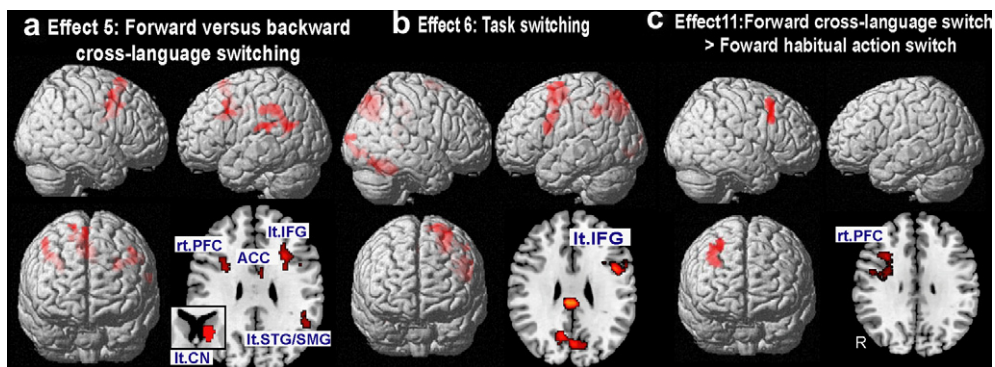


Fig. 3. (a) Brain activity was greater for the forward language switch than for the backward language switch (Effect 5: Forward versus backward cross-language switching). Significant activity was observed in the right prefrontal cortex (rt. PFC), left inferior frontal gyrus (lt. IFG), left superior temporal gyrus/supramarginal gyrus (lt. STG/SMG), anterior cingulate cortex (ACC), and left caudate nucleus (lt. CN). (b) Brain activity representing the effects of Task switching (Effect 6). Significant activity was observed in the lt. IFG, left middle frontal gyrus (dorsal premotor area), left inferior parietal lobe, and right inferior occipital lobe. (c) Brain activity representing Effect 12 (Forward language switch > forward action switch). Significant activity was observed in the rt. PFC. The threshold was set at a height threshold of $p < 0.001$ (uncorrected) and an extent threshold of $p < 0.05$ corrected for multiple comparisons in all the above contrasts.

Table 3

Effect 6: Activities showing significant effects of the task switch condition as compared with the non-switching condition ($p < 0.001$, uncorrected, cluster $p < 0.05$ corrected).

Anatomical location	X	Y	Z	Z-value	Cluster P corrected	KE
Left inferior parietal lobe	-32	-50	40	5.67	0.00	2181
Left middle frontal gyrus(premotor area)	-28	-8	56	4.72	0.00	814
Left inferior frontal gyrus	-50	10	20	4.22	0.00	399
Right infeior occipital gyrus	8	-70	42	4.53	0.00	1016

forward cross-language versus forward action switching effect (Effect 12) in the left STG ($x, y, z = -53, -34, 29; z = 3.23, p = 0.02$ FWE-corrected) and left SMG ($x, y, z = -45, -50, 36; z = 3.00; p = 0.01$ FWE-corrected). See also the plots of task-related activity as a supporting finding (Fig. 4).

3.2.3. Correlation analysis

Behaviorally, there was a significantly negative correlation between RT during the forward language switch condition and the EVT score ($r = -0.61, p = 0.005$), indicating that more proficient subjects more quickly switched from L1 phonology to L2 phonology. The voxel-wise correlation analysis between the effect size of activity for the forward language switch (Effect 3) and the EVT score revealed a significantly positive correlation between the forward language switch-related brain activity and the degree of L2 fluency only in the right PFC (Fig. 5, Table 6). However, the EVT score was not correlated

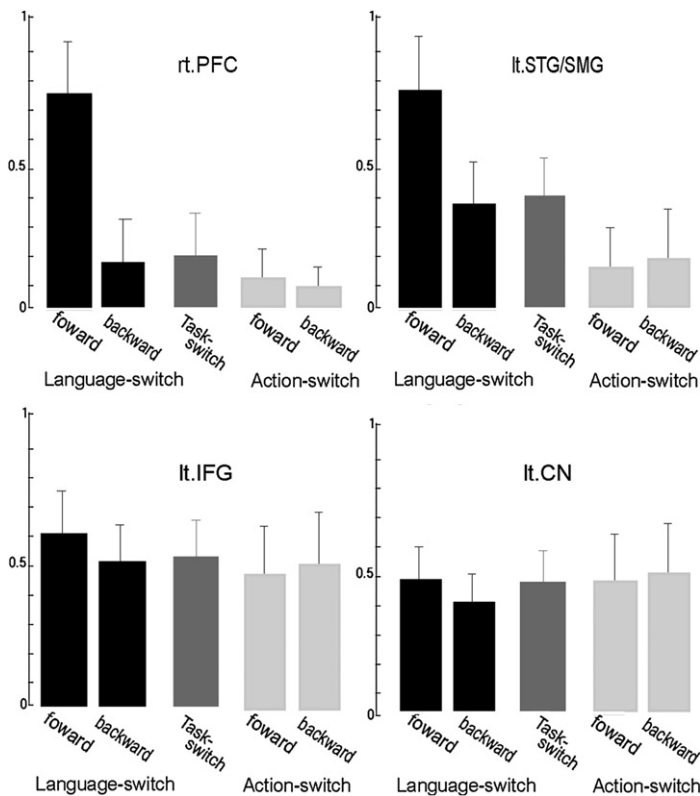


Fig. 4. Plots of switching-related activity (parameter estimates relative to the fixation baseline) for the language switch (forward and backward cross-language switching), the task switch (switching between the phonological and numerical tasks), and the sequence switch (forward and backward habitual-action switching) in the representative areas.

Table 4

(a) Effect 8: Activities showing significant effects of action-sequence switching trials as compared with the non-switch action sequence. (b) Effect 9: Activities showing significant effects of forward habitual-action switch trials as compared with the non-switch action sequence. (c) Effect 10: Activities showing significant effects of backward habitual-action-sequence switch trials as compared with the non-switch action sequence. The threshold was set at a height threshold of $p < 0.001$ (uncorrected) and an extent threshold of $p < 0.05$ corrected for multiple comparisons in all the above contrasts.

Anatomical location	X	Y	Z	Z-value	Cluster P corrected	KE
<i>(a) Effect 8: Action switching</i>						
Left superior parietal lobe	-6	-76	46	5.79	0.00	5604
Left inferior frontal gyrus	-39	20	20	5.46	0.00	7131
Left anterior cingulate cortex	-2	15	25	4.53	0.00	655
Right superior parietal lobe	18	-52	62	5.71	0.00	5604
<i>(b) Effect 9: Forward action switching</i>						
Left inferior frontal gyrus	-52	-12	2	4.31	0.00	383
Left inferior parietal lobe	-54	-34	50	3.39	0.00	246
Left superior occipital lobe	-22	-68	34	3.82	0.00	390
Right anterior cingulate cortex	0	14	26	5.06	0.00	638
Right inferior parietal lobe	54	30	50	4.30	0.00	346
<i>(c) Effect 10: Backward action switching</i>						
Left occipital lobe	-10	-92	2	4.77	0.00	1772
Left inferior frontal gyrus	-52	16	18	4.49	0.00	483
Left inferior parietal lobe	-22	-70	48	4.40	0.00	265
Right anterior cingulate cortex	0	6	2	4.40	0.00	140

Coordinates (x, y, z) indicate local maxima in each brain region according to the Montreal Neurological Institute template.

with the brain activity during the L2_{non-switching} trials (relative to the baseline) or the brain activity during the forward habitual-action switch (Effect 9).

4. Discussion

The subjects in the present study were late bilinguals with various levels of L2 proficiency. Hence, the present results may not be directly comparable to previous language switch studies in which only high proficiency bilinguals were enrolled (Crinion et al., 2006). However, the present bilingual subjects showed no significant differences in brain activity or task performance between L1 and L2 in the non-switching conditions. Thus, the subjects' proficiency in L2 sufficed for performing the phonological judgment with L2 to a comparable degree with L1, at least in the non-switching conditions. Moreover, asymmetry in language proficiency was only evident when brain activity was evaluated for forward versus backward cross-language switch. Because the behavioral data failed to show an asymmetry for the cost of language switch, the asymmetry in brain activity for language switch cannot be ascribed to a difference in task performance.

The main finding of the present study was the demonstration of asymmetry in brain activity sensitive to switching direction of languages for phonological judgment. The comparisons between the forward and backward language switch showed no significantly increased activation for the backward switching. Conversely, relative to the backward cross-language switching, the forward cross-language switching elicited greater activation in the right PFC, left IFG, left STG/SMG, ACC, and caudate nucleus. The left IFG, middle frontal gyrus, ACC, and left caudate nucleus were engaged in cross-language switch, cognitive-task switch, and action-sequence switch. By contrast, converging evidence from the main and action-sequence switch experiments suggested that the right PFC and the left STG/SMG

Table 5

Effect 12: Activities showing significant effects of forward language switch trials as compared with the forward habitual-action switch ($p < 0.001$, uncorrected, cluster $p < 0.05$ corrected).

Anatomical location	X	Y	Z	Z-value	ClusterP corrected	K _E
Right prefrontal cortex	31	15	31	4.43	0.00	490

Coordinates (x, y, z) indicate local maxima in each brain region according to the Montreal Neurological Institute template.

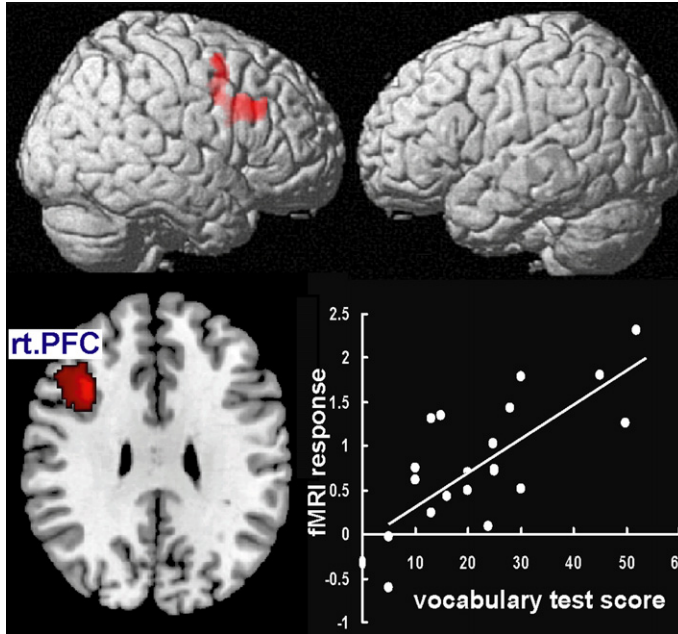


Fig. 5. Three-dimensional render images showing the correlation between the English Vocabulary Test (EVT) score and the effect size of activity for forward language switching. The right prefrontal activity during the forward language condition ($L1-L2_{\text{switch}}$) was correlated with the EVT score reflecting differential levels of L2 proficiency across participants ($p < 0.05$ family-wise error corrected).

were particularly involved in the forward cross-language switching. The asymmetric modulation of neural activity sensitive to the direction of language switch likely reflected asymmetric proficiency or exposure time between L1 and L2 in the present subject group. A recent study has suggested that lexical processing of L2 is compensated by a top-down cognitive switch even in highly proficient bilinguals (Nakamura et al., 2010). In the present study, the dominant L1 should be more actively inhibited (or the weaker L2 more actively retrieved) to allow for smooth switching from a stronger language into a weaker one than switching in the opposite direction. Our results confirmed previous findings that only switching into the weaker language was paralleled by activity in the caudate nucleus, ACC, and PFC regions (Abutalebi, Annoni et al., 2007; Abutalebi, Brambati et al., 2007; Wang et al., 2007).

A previous study showed selective engagement of the right PFC in language switch in a mixed language condition in highly proficient bilinguals (Hernandez et al., 2001). Several other studies also demonstrated the involvement of the PFC in language switch, although activation patterns substantially varied across studies (Abutalebi, 2008; Friederici, 2006; Hernandez et al., 2001; Wang et al., 2007). The present study extended these finding by showing that the right PFC was sensitive to the direction of language switch. Moreover, the right PFC was the only area showing forward cross-language switching-related activity correlated with L2 proficiency in the whole-brain exploratory analysis. Task difficulty hardly accounted for the right PFC activity because the analysis of RTs revealed a significantly negative correlation between the EVT scores and the RTs during forward switching. Stronger involvement of the right PFC in more proficient subjects indicates that forward cross-language

Table 6

Activities showing significant correlation between the English Vocabulary Test (EVT) score and the effect size of activity for the forward language switch. ($p < 0.001$, uncorrected, cluster $p < 0.05$ corrected).

Anatomical location	X	Y	Z	Z-value	Cluster P corrected	K_E
Right prefrontal cortex	34	17	30	5.78	0.00	634

Coordinates (x, y, z) indicate local maxima in each brain region according to the Montreal Neurological Institute template.

switching may depend on active recruitment of neural resources, the right PFC in particular, at least in late bilinguals. There was no correlation of activity during the forward action switching with the EVT scores, supporting that the right PFC was not necessarily involved in general switch to inhibit experienced behaviors. In late bilinguals who have asymmetric proficiency between languages, the right PFC may play a part in switching between languages with selection of phonological representations from the non-dominant language lexicon. Additionally, a recent study reported that acquiring unfamiliar words, an important ability for second language learning, elicited more right prefrontal activation than left in children (Sugiura et al., 2011). The present study has shown for the first time that the engagement of the right PFC in language switching processes may be proficiency dependent. Consistently, the level of L2 proficiency may also be correlated with the gray matter volume of the right PFC as shown in our preliminary study (Hosoda et al., 2009). This finding supports an active role of the right PFC in language switch.

Importantly, the significance of the right PFC for language switch is supported by a case study in which a dextral late bilingual patient involuntary switched between languages after suffering from a lesion in the right PFC (Hecaen, Mazars, Ramier, Goldblum, & Merienne, 1971). It is proposed that, in bilinguals, competition between L1 and L2 is solved by inhibiting non-target languages and/or by activating retrieval processes from the target language. Previous studies suggested that the right PFC might subservise the neural bases of inhibitory control when selecting between two behavioral options (Aron, Robbins, & Poldrack, 2004; Braver et al., 2001). Furthermore, an inhibitory mechanism may be shared between manual and speech acts (Xue, Aron, & Poldrack, 2008). Hence, a question arose whether the right PFC activity represented mechanisms for language switch or more generally for inhibitory control of behavior. Comparing between the cross-language and task switching conditions might not solve this issue because we did not expect behavioral asymmetry between the phonological and numerical tasks. Therefore, we ran an action-sequence switch experiment, which was supposed to involve an inhibitory process to switch from well-trained sequential actions into a newly generated one (forward habitual-action switch). The analysis of Effect 12 (Forward cross-language switching > forward action switching) showed that the right PFC activity was significantly greater during the forward language switch than the forward habitual-action switch. It should be noted that no significant difference in the switching cost was found in the RT analysis between the forward cross-language switching and the forward action switching. This meant that differences in difficulty for switching hardly accounted for the PFC activity in contrast with forward cross-language switching > forward action switching. This analysis suggested that a cognitive component related to inhibition of habitual behavior in general might not explain the activity in the right PFC during the cross-language switching. Rather, the evidence appears to support the possibility that the right PFC region may play a specific role in switching from a strong language to a less solid language.

Alternatively, the present finding on the right PFC may be explained by the hemispheric encoding/retrieval asymmetry model (Tulving, Kapur, Craik, Moscovitch, & Houle, 1994), which claims that the right PFC is involved in retrieval of stored information. For those people who have two competitive (yet unbalanced) lexical representations, retrieving a weaker lexicon will require greater resources than retrieving the stronger lexicon. The inhibitory switch model predicts that strong inhibitory processes are required to overcome interference from L1, and thus higher switching costs are required to shift from L1 to L2 (Green, 1986). Strong inhibition of the dominant language or demanding retrieval of the non-dominant language is needed for the forward language switch unless an individual has equal proficiency between two languages. Collectively, the right PFC may be involved in the selection of phonological representations from non-dominant language lexicon in late bilinguals who have asymmetric proficiency between languages.

Previously, activation of the left STG during L2 tasks was found in highly proficient bilinguals but not in less proficient bilinguals (Khateb et al., 2007; Perani & Abutalebi, 2005). The SMG/STG activity during the forward cross-language, but not during the L2_{non-switch}, implied that activity there was also influenced by task demands. In fact, the role of the left STG/SMG in language switch is supported by many studies (Hernandez et al., 2001; Khateb et al., 2007; Moritz-Gasser & Duffau, 2009; Price et al., 1999). In monolingual studies, the left STG is engaged in linguistic integration and phonological processing connecting an input (orthography) and an output (phonology) in the lexical network (Baldo, Schwartz, Wilkins, & Dronkers, 2006; Price, Moore, Humphreys, & Wise, 1997; Tan et al., 2003). Together, the enhanced activation of the left STG/SMG for the forward language switch in the present

study may be explained by greater demands for converting orthographic information of Arabic numerals into L2 phonology than into L1 phonology.

The ACC is involved in selection of appropriate responses and monitoring of response errors (Badgaiyan & Posner, 1998; Bush, Luu, & Posner, 2000; Kerns et al., 2004; Veen, Cohen, Botvinick, Stenger, & Carter, 2001). This view is consistent with the involvement of the ACC in the task switching and action switching. In addition, a previous bilingual study demonstrated the involvement of the ACC in selection between languages but not in task selection within a language (Abutalebi & Green, 2007). Therefore, in bilinguals, the ACC may be involved in the selection of the appropriate language, monitoring the selection error, and conflict detection, which are all relevant to language switch.

The present results support that the left caudate nucleus subserves language switch (Crinion et al., 2006). Patients with left subcortical lesions involving the caudate nucleus involuntary switch between languages (Abutalebi, Mizzo, & Cappa, 2000; Marien, Abutalebi, Engelborghs, & De Deyn, 2005). The left caudate nucleus is activated when the language processing system cannot rely entirely on automatic mechanisms but has to recruit controlled processes (Friederici, 2006). Highly proficient bilinguals may have more automatic language switch processes recruiting the caudate nucleus than the present late bilinguals in whom conscious language switch might be predominant. The roles of the automatic versus cognitive controls in language switching should be tested in future studies comparing early and late bilinguals.

In the present study, the left IFG showed significant activation in the language switch, task switch, and action-sequence switch. As frequently observed in neuroimaging studies (Price et al., 1999; Thompson-Schill, D'Esposito, & Kan, 1999), activity of the left IFG may be related to selection processes between competing alternatives including different languages. In addition, the left IFG is regarded as a center of executive language functions and is involved in diverse language processes including syntactic processing, selection of phonology, and switching between linguistic tasks. Because left IFG activity is influenced by learning stage or proficiency of different languages (Sakai, 2005; Sakai, Miura, Narafu, & Muraishi, 2004), the IFG functions for language switch should be tested in future studies including both early and late bilinguals. Moreover, the left PFC including the left IFG are also involved in general executive functions (Abe et al., 2007; Cohen, 2000; DiGirolamo et al., 2001; Dosenbach et al., 2006) including task switching (Dove et al., 2000; Hanakawa, 2011). In addition, activity in the left IFG during the sequence switch tasks is consistent with its function for planning and generation of action sequences (Hanakawa et al., 2003). Accordingly, activity of the left prefrontal regions may be related to selection processes between competing alternatives such as different languages (Price et al., 1999; Thompson-Schill et al., 1999), different tasks (Dreher, Koechlin, Ali, & Grafman, 2002), and different action sequences.

The present study indicated that the language switch and sequence/cognitive-task switch might be associated with partially segregated neural underpinnings. The right PFC, left STG/SMG, left IFG, ACC, and left caudate nucleus may contribute differentially to a few behavioral processes underlying language switch in adults with asymmetric proficiency between two languages.

Conflict of interest

The authors declare no conflict of interest.

References

- Abe, M., Hanakawa, T., Takayama, Y., Kuroki, C., Ogawa, S., & Fukuyama, H. (2007). Functional coupling of human prefrontal and premotor areas during cognitive manipulation. *Journal of Neuroscience*, 27(13), 3429–3438.
- Abutalebi, J. (2008). Neural aspects of second language representation and language control. *Acta Psychologica (Amsterdam)*, 128(3), 466–478.
- Abutalebi, J., Annoni, J. M., Zimine, I., Pegna, A. J., Seghier, M. L., Lee-Jahnke, H., et al. (2007). Language control and lexical competition in bilinguals: an event-related fMRI study. *Cerebral Cortex*, .
- Abutalebi, J., Brambati, S. M., Annoni, J. M., Moro, A., Cappa, S. F., & Perani, D. (2007). The neural cost of the auditory perception of language switches: an event-related functional magnetic resonance imaging study in bilinguals. *Journal of Neuroscience*, 27(50), 13762–13769.
- Abutalebi, J., & Green, D. W. (2007). Bilingual language production: the neurocognition of language representation and control. *Journal of Neurolinguistics*, 20, 242–275.

- Abutalebi, J., Mizzo, A., & Cappa, S. (2000). Do subcortical structures control language selection in bilinguals? Evidence from pathological language mixing. *Neurocase*, 6, 101–106.
- Aron, A. R., Robbins, T. W., & Poldrack, R. A. (2004). Inhibition and the right inferior frontal cortex. *Trends in Cognitive Sciences*, 8(4), 170–177.
- Badgaiyan, R. D., & Posner, M. I. (1998). Mapping the cingulate cortex in response selection and monitoring. *Neuroimage*, 7(3), 255–260.
- Baldo, J. V., Schwartz, S., Wilkins, D., & Dronkers, N. F. (2006). Role of frontal versus temporal cortex in verbal fluency as revealed by voxel-based lesion symptom mapping. *Journal of the International Neuropsychological Society*, 12(6), 896–900.
- Brass, M., Ullsperger, M., Knoesche, T. R., von Cramon, D. Y., & Phillips, N. A. (2005). Who comes first? The role of the prefrontal and parietal cortex in cognitive control. *Journal of Cognitive Neuroscience*, 17(9), 1367–1375.
- Braver, T. S., Barch, D. M., Gray, J. R., Molfese, D. L., & Snyder, A. (2001). Anterior cingulate cortex and response conflict: effects of frequency, inhibition and errors. *Cerebral Cortex*, 11(9), 825–836.
- Bush, G., Luu, P., & Posner, M. I. (2000). Cognitive and emotional influences in anterior cingulate cortex. *Trends in Cognitive Sciences*, 4(6), 215–222.
- Chee, M. W., Soon, C. S., & Lee, H. L. (2003). Common and segregated neuronal networks for different languages revealed using functional magnetic resonance adaptation. *Journal of Cognitive Neuroscience*, 15(1), 85–97.
- Cohen, J. (2000). Prefrontal cortex involved in higher cognitive functions. Introduction. *Neuroimage*, 11(5 Pt 1), 378–379.
- Costa, A., & Santesteban, M. (2004). Bilingual word perception and production: two sides of the same coin? *Trends in Cognitive Sciences*, 8(6), 253, author reply 254.
- Crinion, J., Turner, R., Grogan, A., Hanakawa, T., Noppeney, U., Devlin, J. T., et al. (2006). Language control in the bilingual brain. *Science*, 312(5779), 1537–1540.
- DiGirolamo, G. J., Kramer, A. F., Barad, V., Cepeda, N. J., Weissman, D. H., Milham, M. P., et al. (2001). General and task-specific frontal lobe recruitment in older adults during executive processes: a fMRI investigation of task-switching. *Neuroreport*, 12(9), 2065–2071.
- Dosenbach, N. U., Visscher, K. M., Palmer, E. D., Miezin, F. M., Wenger, K. K., Kang, H. C., et al. (2006). A core system for the implementation of task sets. *Neuron*, 50(5), 799–812.
- Dove, A., Pollmann, S., Schubert, T., Wiggins, C. J., & von Cramon, D. Y. (2000). Prefrontal cortex activation in task switching: an event-related fMRI study. *Brain Research Cognitive Brain Research*, 9(1), 103–109.
- Dreher, J. C., Koehlin, E., Ali, S. O., & Grafman, J. (2002). The roles of timing and task order during task switching. *Neuroimage*, 17(1), 95–109.
- French, R. M., & Jacquet, M. (2004). Understanding bilingual memory: models and data. *Trends in Cognitive Sciences*, 8(2), 87–93.
- Friederici, A. D. (2006). What's in control of language? *Nature Neuroscience*, 9(8), 991–992.
- Friston, K. J., Holmes, A. P., Price, C. J., Büchel, C., & Worsley, K. J. (1999). Multisubject fMRI studies and conjunction analyses. *Neuroimage*, 10(4), 385–396.
- Funahashi, S. (2001). Neuronal mechanisms of executive control by the prefrontal cortex. *Neuroscience Research*, 39(2), 147–165.
- Green, D. W. (1986). Control, activation, and resource: a framework and a model for the control of speech in bilinguals. *Brain and Language*, 27(2), 210–223.
- Hanakawa, T. (2011). Rostral premotor cortex as a gateway between motor and cognitive networks. *Neuroscience Research*, (published online).
- Hanakawa, T., Immisch, I., Toma, K., Dimyan, M. A., Van Gelderen, P., & Hallett, M. (2003). Functional properties of brain areas associated with motor execution and imagery. *Journal of Neurophysiology*, 89(2), 989–1002.
- Hecaen, H., Mazars, G., Ramier, A. M., Goldblum, M. C., & Merienne, L. (1971). Crossed aphasia in a right-handed bilingual (Vietnamese-French) subject. *Revue Neurologique(Paris)*, 124(4), 319–323.
- Hernandez, A. E., Dapretto, M., Mazziotta, J., & Bookheimer, S. (2001). Language switching and language representation in Spanish-English bilinguals: an fMRI study. *Neuroimage*, 14(2), 510–520.
- Hernandez, A. E., Martinez, A., & Kohnert, K. (2000). In search of the language switch: An fMRI study of picture naming in Spanish-English bilinguals. *Brain and Language*, 73(3), 421–431.
- Hosoda, C., Hanakawa, T., Tanaka, S., Nariai, T., Ohno, K., & M, Honda (2009). In N. Research (Ed.), *Correlation between cortico-subcortical gray matter volume and proficiency in second language* (pp. 242). Nagoya, Japan: Japan Neuroscience Society.
- Kerns, J. G., Cohen, J. D., MacDonald, A. W., 3rd, Cho, R. Y., Stenger, V. A., & Carter, C. S. (2004). Anterior cingulate conflict monitoring and adjustments in control. *Science*, 303(5660), 1023–1026.
- Khateb, A., Abutalebi, J., Michel, C. M., Pegna, A. J., Lee-Jahnke, H., & Annoni, J. M. (2007). Language selection in bilinguals: a spatio-temporal analysis of electric brain activity. *International Journal of Psychophysiology*, 65(3), 201–213.
- Kho, K. H., Duffau, H., Gatignol, P., Leijten, F. S., Ramsey, N. F., van Rijen, P. C., et al. (2007). Involuntary language switching in two bilingual patients during the Wada test and intraoperative electrocortical stimulation. *Brain and Language*, 101(1), 31–37.
- Kimberg, D. Y., Aguirre, G. K., & D'Esposito, M. (2000). Modulation of task-related neural activity in task-switching: an fMRI study. *Brain Research Cognitive Brain Research*, 10(1–2), 189–196.
- Macnamara, J., Krauthammer, M., & Bolgar, M. (1968). Language switching in bilinguals as a function of stimulus and response uncertainty. *Journal of Experimental Psychology*, 78(2), 208–215.
- Marien, P., Abutalebi, J., Engelborghs, S., & De Deyn, P. P. (2005). Pathophysiology of language switching and mixing in an early bilingual child with subcortical aphasia. *Neurocase*, 11(6), 385–398.
- Meuter, R. F. I., & Allan, A. (1999). Bilingual Language Switching in Naming: Asymmetrical Costs of Language Selection. *Journal of Memory and Language*, 40, 25–40.
- Moritz-Gasser, S., & Duffau, H. (2009). Evidence of a large-scale network underlying language switching: a brain stimulation study. *Journal of Neurosurgery*, 111(4), 729–732.
- Nakamura, K., Kouider, S., Makuuchi, M., Kuroki, C., Hanajima, R., Ugawa, Y., et al. (2010). Neural Control of Cross-language Asymmetry in the Bilingual Brain. *Cerebral Cortex*, .
- Perani, D., & Abutalebi, J. (2005). The neural basis of first and second language processing. *Current Opinion in Neurobiology*, 15(2), 202–206.
- Price, C. J., Green, D. W., & Von Studnitz, R. (1999). A functional imaging study of translation and language switching. *Brain*, 122(Pt 12), 2221–2235.

- Price, C. J., Moore, C. J., Humphreys, G. W., & Wise, R. J. S. (1997). Segregating semantic from phonological processes during reading. *Journal of Cognitive Neuroscience*, 9(6), 727–733.
- Quaresima, V., Ferrari, M., van der Sluijs, M. C., Menssen, J., & Colier, W. N. (2002). Lateral frontal cortex oxygenation changes during translation and language switching revealed by non-invasive near-infrared multi-point measurements. *Brain Research Bulletin*, 59(3), 235–243.
- Rodriguez-Fornells, A., Van der Laugt, A., Rotte, M., Britti, B., Heinze, H.-J., & Münte, T. F. (2005). Second language interferes with word production in fluent bilinguals: brain potential and functional imaging evidence. *Journal of Cognitive Neuroscience*, 17, 422–433.
- Sakai, K. L. (2005). Language acquisition and brain development. *Science*, 310(5749), 815–819.
- Sakai, K. L., Miura, K., Narafu, N., & Muraishi, Y. (2004). Correlated functional changes of the prefrontal cortex in twins induced by classroom education of second language. *Cerebral Cortex*, 14(11), 1233–1239.
- Sugiura, L., Ojima, S., Matsuba-Kurita, H., Dan, I., Tsuzuki, D., Katsura, T., et al. (2011). Sound to language: different cortical processing for first and second languages in elementary school children as revealed by a large-scale study using fNIRS. *Cerebral Cortex*, (published online).
- Tan, L. H., Spinks, J. A., Feng, C. M., Siok, W. T., Perfetti, C. A., Xiong, J., et al. (2003). Neural systems of second language reading are shaped by native language. *Human Brain Mapping*, 18(3), 158–166.
- Thompson-Schill, S. L., D'Esposito, M., & Kan, I. P. (1999). Effects of repetition and competition on activity in left prefrontal cortex during word generation. *Neuron*, 23(3), 513–522.
- Tulving, E., Kapur, S., Craik, F. I., Moscovitch, M., & Houle, S. (1994). Hemispheric encoding/retrieval asymmetry in episodic memory: positron emission tomography findings. *Proceedings of the National Academy of Sciences of the United States of America*, 91(6), 2016–2020.
- Veen, V., Cohen, J. D., Botvinick, M. M., Stenger, V. A., & Carter, C. S. (2001). Anterior cingulate cortex, conflict monitoring, and levels of processing. *Neuroimage*, 14(6), 1302–1308.
- Venkatraman, V., Siong, S. C., Chee, M. W., & Ansari, D. (2006). Effect of language switching on arithmetic: a bilingual fMRI study. *Journal of Cognitive Neuroscience*, 18(1), 64–74.
- Wang, Y., Xue, G., Chen, C., Xue, F., & Dong, Q. (2007). Neural bases of asymmetric language switching in second-language learners: an ER-fMRI study. *Neuroimage*, 35(2), 862–870.
- Xue, G., Aron, A. R., & Poldrack, R. A. (2008). Common neural substrates for inhibition of spoken and manual responses. *Cerebral Cortex*, 18(8), 1923–1932.
- Xue, G., Dong, Q., Jin, Z., Zhang, L., & Wang, Y. (2004). An fMRI study with semantic access in low proficiency second language learners. *Neuroreport*, 15(5), 791–796.