

Neural Control of Cross-language Asymmetry in the Bilingual Brain

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Most bilinguals understand their second language more slowly than their first. This behavioral asymmetry may arise from the perceptual, phonological, lexicosemantic, or strategic components of bilingual word processing. However, little is known about the neural source of such language dominance and how it is regulated in the bilingual brain. Using functional magnetic resonance imaging, we found that unconscious neural priming in bilingual word recognition is language nonselective in the left midfusiform gyrus but exhibits a preference for the dominant language in the left posterior middle temporal gyrus (MTG). These early-stage components of reading were located slightly upstream of the left midlateral MTG, which exhibited enhanced response during a conscious switch of language. Effective connectivity analysis revealed that this language switch is triggered by reentrant signals from inferior frontal cortex and not by bottom-up signals from occipitotemporal cortex. We further confirmed that magnetic stimulation of the same inferior frontal region interferes with conscious language control but does not disrupt unconscious priming by masked words. Collectively, our results demonstrate that the neural bottleneck in the bilingual brain is a cross-language asymmetry of form-meaning association in inferolateral temporal cortex, which is overcome by a top-down cognitive control for implementing a task schema in each language.

Keywords: bilingualism, effective connectivity, fMRI, language dominance, repetition priming, transcranial magnetic stimulation

Introduction

A large proportion of literate people in the world are estimated to understand written text in a nonnative language (De Bot and Kroll 2002). Bilingual literacy in the broad sense is a common cultural skill that relies on the “metalinguistic” knowledge acquired through the first language (L1) (Cummins 1991). At the neural level, such language-independent cognitive components are represented as a common left-hemisphere network engaged by both L1 and a second language (L2) (Chee et al. 1999; Price et al. 1999). However, this cerebral network for reading should operate differently between the dominant and nondominant languages since it has been shown that even proficient bilinguals are slower to recognize L2 than L1 (Grainger and Beauvillain 1987; Jiang 1999; Thomas and Allport 2000). That is, it is open whether and to what extent the bilingual brain can decode L2 automatically without effortful cognitive control.

Several behavioral studies suggest that language selection during reading consists of a stimulus-driven activation of a target language (Grainger and Beauvillain 1987; Tzeglou et al. 1996)

and a subsequent inhibition of other languages without the mediation of strategic control (Dijkstra and Van Heuven 2002). Indeed, an event-related potential study suggests that bilinguals quickly filter out a nontarget language even before accessing lexical information (Rodriguez-Fornells et al. 2002). Such bottom-up activation and local inhibitory control may occur within the left occipitotemporal cortex since this region is involved in an early and unconscious stage of reading (Dehaene et al. 2001) and is sensitive to language-specific orthographic patterns (Nakamura et al. 2005; Vinckier et al. 2007).

However, other behavioral studies propose that bilinguals need to make a conscious effort to suppress the interference from a nontarget language during visual word recognition (Green 1998; Thomas and Allport 2000). Here, the selection of a required language is assumed to be a form of intended action that is achieved at a later stage of reading by implementing a task set specific to the input language. This top-down, voluntary regulation model seems consistent with the brain imaging and neuropsychological data showing that the left inferolateral frontal cortex is involved in “language switching,” at least for speech production (Fabbro et al. 2000; Hernandez et al. 2001) and reading aloud (Price et al. 1999). However, the extent of prefrontal contribution during bilingual word recognition is still unclear because the nature and amount of strategic control may change drastically when behavioral tasks require an overt spoken response (Green 1998; Reynolds and Besner 2006; Nakamura et al. 2007).

In fact, recent brain imaging work with L1 users suggests that stimulus-induced activation by visual words propagates along feed-forward connections in the ventral processing stream (Nakamura et al. 2007) and is then amplified by reentrant top-down signals from the frontoparietal attentional network (Dehaene et al. 2001; Kouider and Dehaene 2007). For bilinguals, however, the bottom-up processing of letter strings may tap different levels of representations between L1 and L2 since the occipitotemporal region involved in object recognition is sensitive to the perceptual familiarity of stimuli (Henson et al. 2000) and the level of visual expertise (Gauthier et al. 2000). The left occipitotemporal cortex may also exhibit differential sensitivity to L2 because the region is thought to house meaning-level representations (Chertkow et al. 1997; Devlin et al. 2004; Nakamura et al. 2007). For example, behavioral studies have suggested that L2 words are more weakly connected to the semantic system than L1 words (Kroll and Tokowicz 2001). Or rather, reading in L2 may rely not on direct lexicosemantic activation but on some indirect cognitive pathways, for example, letter-to-sound translation (Rodriguez-Fornells et al. 2002) since the robustness of phonological

activation might be constant regardless of the level of language proficiency (Duyck et al. 2004). In turn, such cross-language asymmetry in strategic control should change the interregional connection strength in the entire cerebral language network (Bitan et al. 2005; Nakamura et al. 2006).

Using a cross-language priming paradigm (Fig. 1), we explored the functional architecture of the cerebral reading system in Japanese–English bilinguals. Visual recognition of a target word is known to be facilitated after a brief, subliminal

exposure to the same word or “prime” (Forster et al. 2003). For bilinguals, such response facilitation does occur for translation equivalents across languages, even when primes and targets are written in radically different formats, such as “telephone” and “電話” (Gollan et al. 1997; Jiang 1999; Finkbeiner et al. 2004). We first isolated the automatic cerebral components of bilingual word recognition using functional magnetic resonance imaging (fMRI) since our masked priming procedure allows extracting bottom-up neural activation during reading by minimizing strategic or attentional effects (Naccache and Dehaene 2001; Forster et al. 2003). Moreover, since our mixed-language design involved unpredictable changes of target script between trials, we then identified phasic neural activations occurring when participants consciously switched from one language to another. Using dynamic causal modeling (Friston et al. 2003) and transcranial magnetic stimulation (TMS), we further tested the functional connectivity between these automatic and voluntary neural components during bilingual word recognition.

Materials and Methods

Participants

Thirty-six right-handed Japanese speakers participated in the present study (24 participants for the fMRI experiment (age range = 21–29 years, 8 females) and 12 participants for the TMS experiment (age range = 21–38 years, 3 females). None of these participants received both experiments. All were students or staff members at the University of Tokyo and had received more than 8 years of formal training in English after the age of 10 years. At least an intermediate-level command of spoken and written English is required for undergraduate admission at the University of Tokyo. In addition, the overall Test of English for International Communication (<http://www.ets.org>) score for postgraduate students is estimated to fall in the range of 700–800 according to a recent survey by the University Cooperative Association. In a pretest interview, all participants reported regular use of English, more often written than spoken, for their professional or academic activities and judged themselves to be relatively proficient in their L2. We considered the daily exposure to written texts as a key inclusion criterion for selecting participants for the present study since our primary goal was to explore the neural control of bilingual visual word recognition. All participants gave written informed consent prior to the fMRI or TMS experiments. The protocol of this study was approved by the ethical committee of the University of Tokyo.

Materials and Procedures

The visual stimuli consisted of 96 high-frequency English nouns and their translation equivalents in Japanese logograms. These items were polarized according to the concreteness rating of the MRC psycholinguistic database such that half of them represented concrete objects (e.g., telephone) and the other half abstract concepts (e.g., rule). English primes were masked by a sequence of 8 hash marks, whereas Japanese primes were masked by 3 arrays of 10 square and 10 circles. Primes were two-thirds the size of targets of the same language. Primes and targets always belonged to a same category, thereby minimizing any potential differences in motor response bias between repeated and unrepeated trials. Participants were not informed about the presence of prime words. They pressed an optical key as quickly as possible to indicate whether target words denoted concrete objects or abstract ideas.

In the fMRI experiment, participants received 4 sessions of 240 randomly ordered trials (24 trials for each priming condition plus 48 trials for a word-absent baseline). For the TMS experiment, participants performed 2 sessions of the same categorization task without the baseline. The mixed-language paradigm produced a rapid and unpredictable change of target script between 2 consecutive trials with a probability of approximately 50%. Therefore, participants needed to

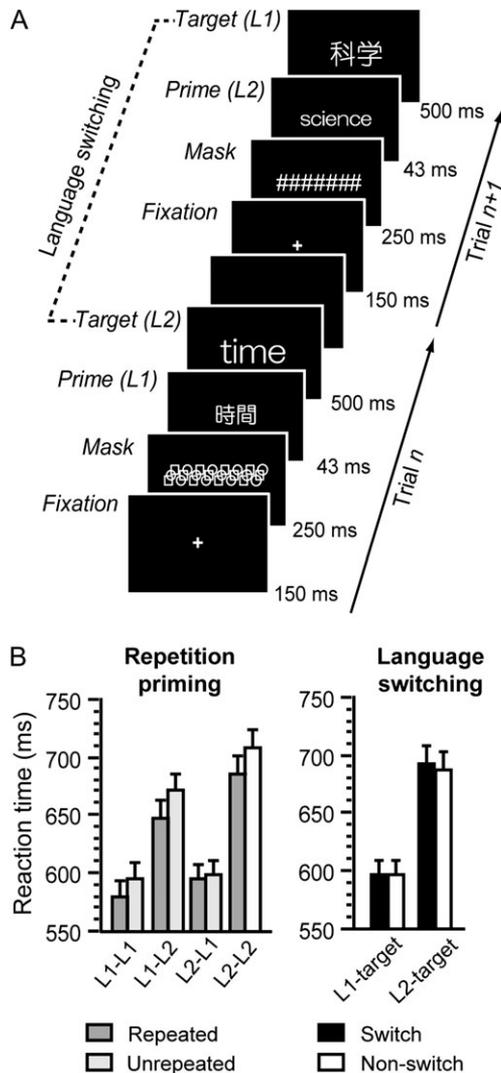


Figure 1. Experimental paradigm and behavioral results. (A) Event sequence used for the fMRI and TMS experiments. Each trial consisted of a masked prime and a visible target, each written in either L1 or L2 scripts. The prime–target relation could be either identical or unrelated in the same language and either equivalent or unrelated in different languages. Participants made a concrete/abstract judgment about a target word in each trial. The script type of visible targets could change unpredictably from one trial to the next under this mixed-language design. Thus, participants needed to switch consciously from one language to another when target script changed between 2 consecutive trials. (B) Behavioral effects of repetition priming and language switching (across-participant mean reaction time \pm standard error of the mean). Left: participants responded more quickly when targets were preceded by the same words in the same language, be it L1 or L2 (within-language priming) and when L2 targets were preceded by their translation equivalents in L1 (cross-language priming). However, this unconscious response facilitation did not occur when L1 targets were primed by their L2 equivalents. Right: language-switch trials produced no additional delay in behavioral response relative to nonswitch trials, irrespective of the type of target language.

consciously switch from one language to another when the script type of visible targets shifted from one trial to the next.

This cross-language priming paradigm was arranged in a $2 \times 2 \times 2$ factorial design treating prime-target relation (repetition/translation and unrelated control), prime language (L1 and L2), and target language (L1 and L2) as within-participant factors. We estimated the behavioral effects of voluntary language selection with a separate 2×2 factorial design treating target language (L1 and L2) and its between-trial changes (switch and nonswitch) as main factors.

Prior to the main experiments, we conducted a behavioral piloting study to evaluate the visibility of primes with a separate group of 16 participants. Each trial included the same sequence of masks and words as in the activation paradigm, except that the primes appeared as left-right inverted words with a probability of 50%. Participants were asked to determine whether primes were flipped or not without time pressure (64 trials). For each participant, a prime visibility index (d') was computed by treating the regular words and the inverted words as signal and noise, respectively, and then submitted to a group-level analysis using t -statistics. The overall mean of this behavioral measure was 0.05 and did not depart significantly from 0 ($t = 1.24$, $P > 0.2$), suggesting that participants did not perceive masked primes consciously. The prime visibility did not differ between the 2 prime languages ($t = 1.44$, $P > 0.15$) or between within- and cross-language conditions ($t = 1.51$, $P > 0.15$).

fMRI Procedures

The experiment was conducted using a Siemens Allegra 3-T head scanner using a standard head coil optimized for a gradient echo-echo planar imaging sequence (25 contiguous axial slices, thickness = 5 mm with 1 mm gap, time repetition = 1400 ms, time echo = 30 ms, flip angle = 80° , field of view = $256 \times 256 \text{ mm}^2$, 64×64 pixels). High-resolution anatomical images were obtained prior to the main experiment. Four scanning sessions, each lasting 11 min 16 s and giving 483 volumes, were performed.

Data Analysis

After image reconstruction, the fMRI data were processed using SPM2 (Wellcome Department of Cognitive Neurology, London, UK). Three initial images were discarded to eliminate nonequilibrium effects of magnetization. Images were corrected for head motion, normalized to the standard brain space, and spatially smoothed with an isotropic Gaussian filter (5-mm full width at half maximum). These images were then high-pass filtered at 120 s and smoothed with a 4-s Gaussian kernel.

Group-based statistical inference was made using a random-effect model. For each participant, a weighted mean image for each contrast was computed by fitting each voxel time series with the known time series of the 9 event types convolved with a canonical hemodynamic response function with time and dispersion derivatives. We first determined the brain regions engaged by both L1 and L2 by contrasting the 8 priming conditions with the word-absent baseline. All subsequent analyses were made in this shared network for reading (inclusive masking at $P < 0.005$). The effects of neural response adaptation, or repetition suppression, were calculated as the reduction of activation in repeated trials relative to nonrepeated trials (Henson and Rugg 2003). Unless stated otherwise, all effects of interest were tested voxel level at $P < 0.001$ with an extent threshold of 20 or more contiguous voxels. Voxel coordinates are reported according to the stereotaxic atlas of Talairach and Tournoux (1988).

For the analysis of effective connectivity, we created a 6-mm radius volume of interest at the fusiform gyrus (FG) showing within-language priming and at the left midlateral middle temporal gyrus (MTG) involved in conscious language switch. Based on the known role of the inferior frontal cortex in task switching (Brass et al. 2005), we further identified a peak activation in the left inferior frontal gyrus (IFG) within the cerebral reading network (voxel-level threshold $P < 10^{-6}$). For each participant, regional responses were extracted for each session by calculating the principal eigenvariate across all voxels within the 6-mm sphere centered at the most significant voxel in the random-effects analyses. Using the 2×2 design matrix with target language and switching, we constructed a fully interconnected model to compute

the connectivity parameters representing the intrinsic strength of interregional connections and their stimulus-dependent modulations. For each of the interregional coupling, the connection parameters from 4 sessions were collapsed per participant and submitted to a second-level analysis. For modulatory effects, the bilinear coupling parameters were submitted to repeated-measures analysis of variance (ANOVA) treating target language and switching as within-participant factors (Bonferroni corrected for multiple comparisons).

TMS Procedures

A high-resolution anatomical MRI scan was obtained for each participant prior to the TMS session. Based on the results from the fMRI experiment, we selected the left posterior MTG and IFG as the target structures to assess the regional specific effects of TMS on repetition priming and those on language switching. The cortical targets for each participant were determined by inverse normalizing the peak coordinates derived from the fMRI results onto the native brain space. A single-pulse TMS was generated using 2 MagStim 200 magnetic stimulators connected to a 70-mm figure-of-8 coil through a BiStim module (Magstim, Whitland, UK). The magnetic pulse has a rise time of 100 μs and a duration of 1 ms. The coil was kept tangential to the skull for stimulating the MTG and IFG with the handle pointing backward parallel to the midline. The TMS pulse was synchronized to the onset of target words and applied at an intensity of 70% of the stimulator power output. A single magnetic pulse at this stimulus intensity is estimated to suppress the local neuronal activity for approximately 100–200 ms (Moliadze et al. 2003). Using a 3-D navigation system (Nexstim, Helsinki, Finland), we tracked the position and orientation of the coil relative to the head at the rate of approximately 20 Hz to minimize their mutual displacement during the TMS session.

Results

fMRI Experiment

Behavioral Results

The mean error rate during semantic categorization was 6.69%. Median reaction times for correct responses were analyzed separately for the effects of masked priming and for those of language switching (Fig. 1B). We first examined the repetition priming effects with a $2 \times 2 \times 2$ ANOVA with prime-target relation, prime-language, and target-language as within-participant factors. Overall, participants responded 77 ms faster to L1 targets than L2 targets ($F_{1,23} = 185.39$, $P < 0.001$).

The existence of an automatic component of reading was indexed by a robust main effect of subliminal priming ($F_{1,23} = 47.83$, $P < 0.001$, collapsed across 4 types of script change). These effects interacted with each other ($F_{1,23} = 33.71$, $P < 0.001$), suggesting a greater savings effect for L2. The unconscious priming was significant when words were repeated in the same language, for both L1 ($F_{1,23} = 18.38$, $P < 0.001$) and L2 ($F_{1,23} = 16.60$, $P < 0.001$). This within-language priming did not differ in effect size between L1 and L2 ($F < 1$) despite the clear advantage of L1 in overt behavioral response. By contrast, participants responded more quickly when L2 targets were preceded by their translation equivalents in L1 ($F_{1,23} = 26.61$, $P < 0.001$) but not when L1 targets were preceded by their L2 equivalents ($F_{1,23} = 0.95$, $P = 0.33$). Indeed, this cross-language priming was significantly greater for the L1-L2 direction than for the L2-L1 direction ($F_{1,23} = 14.82$, $P < 0.005$). The absence of L2-L1 cross-language priming replicates past behavioral studies with different bilingual populations (Gollan et al. 1997; Jiang 1999).

We then searched for a behavioral cost of language switching that may occur when bilinguals shift from one language to

another during conscious word processing (Thomas and Allport 2000). We used a separate 2×2 ANOVA with target language (L1 and L2) and its between-trial alternations (switch and nonswitch) by assuming that such code switching occurred when the type of target language changed relative to its immediately preceding trials. This second analysis revealed that the response time to targets was not affected by the conscious switch of language ($F_{1,23} = 2.67$, $P = 0.12$), thus replicating the results from some behavioral studies (Caramazza and Brones 1980; Potter et al. 1984).

fMRI Results

Brain regions engaged by both languages extended from the bilateral occipitotemporal cortex to the left inferior parietal, left lateral prefrontal, and bilateral medial frontal areas. This common cerebral network for reading included several regions showing differential activation between L1 and L2 (Table 1). We examined neural priming effects, or repetition-induced activation reduction, using a $2 \times 2 \times 2$ factorial model treating prime-target relation, prime-language, and target language as within-participant factors. The main effect of priming was significant only at the left posterior MTG ($Z = 3.52$, Fig. 2). This region exhibited significant or marginally significant effects of repetition suppression for the L1-L1 ($P < 0.05$, corrected for the search volume), L1-L2 ($P < 0.08$), and L2-L2 conditions ($P < 0.003$) but not for the L2-L1 condition ($P > 0.4$), mirroring the pattern of behavioral priming.

However, when restricted to within-language trials, neural priming was found more broadly from the left lateral occipital cortex to the left MTG (Table 2). Notably, the left FG previously associated with abstract orthographic codes (Cohen et al. 2002) exhibited repetition suppression for both the L1-L1 and L2-L2 conditions ($P < 0.003$ and $P < 0.002$, respectively), whereas the magnitude of priming did not differ between the 2 languages ($P > 0.1$). However, this region exhibited no cross-language priming, either in the L1-L2 or L2-L1 directions ($P > 0.4$ for both). Indeed, the FG exhibited greater repetition suppression in within-language trials than in cross-language trials ($Z = 4.72$), suggesting that the region is sensitive only to words repeated in the same language but not to translation equivalents across different languages.

Guided by behavioral models of bilingual reading (Dijkstra and Van Heuven 1998; Green 1998), we also looked for brain areas encoding language membership (L1 or L2) by calculating the

reduction of activation in within-language trials relative to cross-language trials. This neural priming associated with abstract language identity was found at the left medial MTG (12 voxels; $-32, -51, -13$; $Z = 3.34$), which partially overlapped the left occipitotemporal region showing within-language priming.

We then searched for brain regions involved in conscious language selection by using a separate 2×2 factorial model with target language (L1 and L2) and its between-trial alternations (switch and nonswitch). Despite the lack of behavioral cost, the neural effect of language switch was detected as an enhanced response at a midlateral segment of the left MTG approximately 14 mm anterior to the FG (22 voxels, $Z = 4.12$, Fig. 2), which was greater for switching to L2 than for switching to L1 ($Z = 3.22$). The FG exhibited a nonsignificant trend of activation in switch relative to nonswitch trials ($Z = 2.88$). We further tested the same

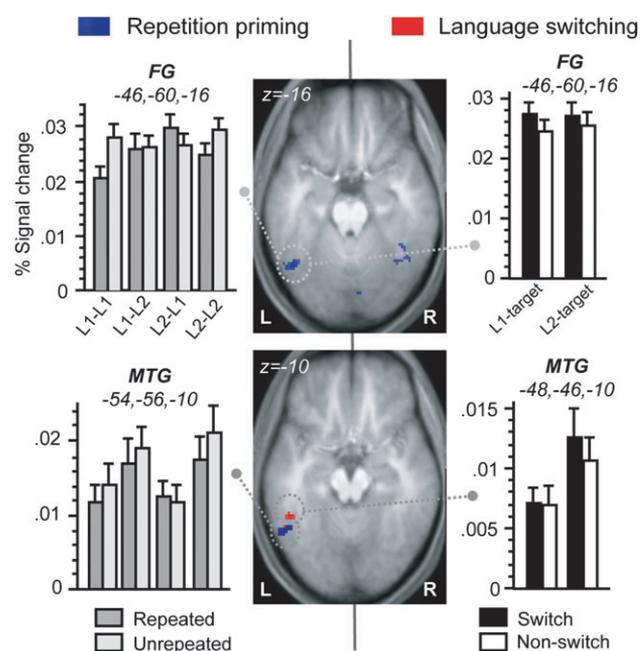


Figure 2. Neural effects of repetition priming and language switching. The left FG exhibited repetition suppression when primes and targets were presented in the same language. Note that the magnitude of this neural priming is almost identical between L1 and L2. The left posterior MTG showed repetition suppression not only in these within-language conditions but also in the L1-L2 cross-language condition, mirroring the pattern of behavioral priming effects. On the other hand, a more anterior segment of the left MTG exhibited transient activation in language-switch trials relative to nonswitch trials ($Z = 4.12$). The FG exhibited only a nonsignificant trend of activation during switching ($Z = 2.88$). The magnitude of cerebral activation (\pm standard error of the mean) was calculated relative to the word-absent baseline for each condition.

Table 1

Brain regions showing differential activation to L1 and L2

Brain region	Coordinate			Maximum Z score	Voxel count
	x	y	z		
L2 > L1					
L lateral frontal area	-42	7	27	6.25	2267
Bil occipital pole	-2	-91	0	5.58	203
Bil medial frontal area	-6	18	45	5.56	1441
L inferior parietal lobe	-32	-54	45	5.56	1529
Bil basal ganglia	12	6	0	5.44	2155
R lateral prefrontal area	36	19	-4	5.44	425
Bil cerebellum	16	-84	-13	5.28	975
L occipitotemporal cortex	-55	-63	-10	4.80	406
R inferior parietal lobe	30	-60	42	4.73	67
L1 > L2					
L medial fusiform area	-28	-38	-20	3.95	41
R medial fusiform area	36	-46	-18	3.45	23

Note: L, left; bil, bilateral; R, right.

Table 2

Brain regions showing within-language priming

Brain region	Coordinate			Maximum Z score	Voxel count
	x	y	z		
L FG/MTG	-46	-61	-15	4.78	97
L lateral occipital area	-38	-89	3	4.24	235
Bil cerebellum	6	-80	-16	4.13	88
R MTG	42	-47	-11	3.99	87
R lateral occipital area	30	-97	1	3.75	72
R thalamus	4	-19	12	3.65	36

Note: L, left; bil, bilateral; R, right.

contrast at a posterior part of the left IFG showing robust activation during semantic categorization ($-50, 6, 32; Z = 6.42$). This posterior inferior frontal region has been previously associated with the regulation of languages in bilinguals (Price et al. 1999; Hernandez et al. 2001) and, more generally, with the cognitive control during task switching (Brass et al. 2005). However, the IFG exhibited only a weak trend of response increase associated with language switch ($Z = 2.08$).

Effective Connectivity Analysis

The code-switching effect in the MTG could be triggered immediately after word identification in occipitotemporal cortex, but it could also reflect reentrant signals associated with a strategic reconfiguration of the cerebral language network. To address this question, we estimated the amount of bottom-up and top-down signal to the MTG during language switching by using a dynamic causal model comprising the FG and IFG. We computed the changes of interregional connection strengths as a function of target language (L1 and L2) and its between-trial switching (switch and nonswitch). Overall, the IFG and MTG exhibited greater positive coupling for L2 relative to L1 for both the forward ($P < 0.001$) and backward ($P < 0.05$) projections (Fig. 3). Critically, this asymmetric interregional coupling exhibited a crossover interaction with language switch, suggesting inhibitory and excitatory modulations on L1 and L2, respectively ($P < 0.003$ for MTG-IFG and $P < 0.03$ for IFG-MTG). By contrast, the reciprocal connections between the MTG and FG did not change with target language ($P > 0.1$ for FG-MTG and $P > 0.06$ for MTG-FG) or with

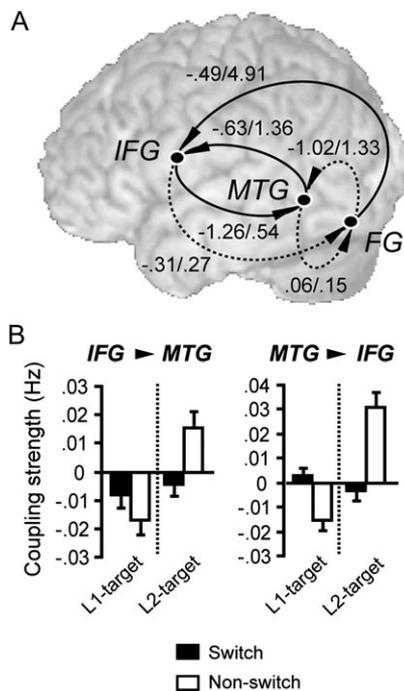


Figure 3. Effective connectivity in the bilingual reading system. (A) Global effects of language. L2 targets increased reciprocal excitatory connections between the MTG and IFG and a bottom-up excitatory input from the FG to the IFG relative to L1 targets. All other dotted lines represent nonsignificant changes in coupling strength. The values next to each arrow indicate the mean connection strength (in 10^{-2} Hz) for each language (L1/L2). (B) Language-by-switching interaction in the IFG-MTG circuitry. Switch trials exerted a differential impact on the IFG-MTG coupling between 2 languages, with a slight increase for L1 targets and a large decrease for L2 targets.

switching ($P > 0.1$ for both directions), suggesting a meager bottom-up contribution to the language switching effect observed at the MTG. The IFG received greater excitatory input from the FG for L2 relative to L1 ($P < 0.001$), which increased in switching trials relative to nonswitching trials ($P < 0.001$). However, the backward IFG-FG projection neither differed between 2 languages ($P > 0.1$) nor changed with switching ($P > 0.1$).

TMS Experiment

We next used TMS to assess the causal influences of bottom-up and top-down signals on repetition priming and language switching (Fig. 4). Participants performed the same categorization task, while a single magnetic pulse was delivered to either the IFG or MTG under a 3-D navigation system. We selected the posterior MTG as the target structure in occipitotemporal cortex since the effects of TMS are usually limited to superficial cortical regions (Walsh and Cowey 2000).

Participants made few errors during the semantic categorization task (mean error rate = 5.17%). We first examined the regional specific impact of TMS on masked priming using a 2×2 ANOVA with repetition (repeated and unrepeated) and stimulation site (MTG and IFG) as within-participant factors. The main effects of repetition and stimulation site were both nonsignificant (F 's < 1) but interacted with each other ($P = 0.03$). Indeed, planned comparisons for each site revealed that the global priming effect survived the stimulation of the IFG ($P < 0.03$) but was eliminated by the stimulation of the MTG ($F < 1$). In contrast, repetition priming was significant for L2 ($P < 0.02$) but not for L1 ($F < 1$) when TMS was delivered to the IFG. This between-language difference was marginally significant ($P < 0.07$), probably reflecting the greater savings effect for L2 (see Fig. 1B).

We then ran a separate $2 \times 2 \times 2$ ANOVA treating target language (L1 and L2), its between-trial change (switch and nonswitch), and site (MTG and IFG) as within-participant factors. Again, participants responded more quickly to L1 than to L2 ($P < 0.001$). The main effects of switching and site and their interaction were all nonsignificant ($P > 0.15$ for all effects). However, we found a significant 3-way interaction between these factors ($P = 0.007$). That is, TMS affected switching to L2

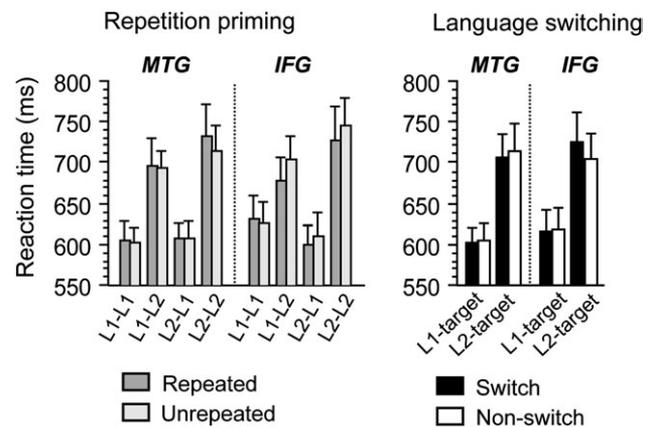


Figure 4. Behavioral effects of TMS on repetition priming and switching. Left: magnetic stimulation of the MTG, but not that of the IFG, eliminated the effects of repetition priming systematically across the 4 priming conditions. Right: magnetic stimulation of the IFG, but not that of the MTG, produced a significant delay when participants switched from L1 to L2.

differently between MTG and IFG ($P < 0.05$), while this switching-by-site interaction never reached significance for L1 ($F < 1$). Moreover, magnetic stimulation of the IFG tended to slow down the participants' response to L2 in switching trials relative to nonswitching trials ($P = 0.08$), whereas this was not the case for the MTG ($F < 1$). No such interference with switching occurred for L1 ($F < 1$ for both sites).

Discussion

A current cognitive model of bilingual word recognition proposes a dual-route connection hypothesis whereby words in L1 and those in L2 are directly linked at the lexical level and indirectly linked through a shared semantic system (Kroll and Tokowicz 2001). Behavioral studies further suggest that these lexicosemantic connections mediate across-language facilitation in conscious word processing (Keatley et al. 1994; Altarriba and Mathis 1997). Our results revealed that the behavioral cross-language priming was represented as reduced activation of the left MTG but not the FG. Moreover, the MTG may play a causal role in the generation of masked priming because the stimulation of the same region disrupted both within- and cross-language effects. Given the cognitive architecture of bilingual memory, these results are overall in accordance with the neuropsychological and brain imaging data showing that the left lateral temporal cortex is involved in lexicosemantic processing during reading (Chertkow et al. 1997; Cohen et al. 2002; Dronkers et al. 2004).

Importantly, the observed effect of unconscious cross-language priming should be attributed to the lexical-level connections between L1 and L2, rather than to the semantic-level link as emphasized by previous behavioral studies (Grainger and Frenck-Mestre 1998; Finkbeiner et al. 2004). This is because masked repetition priming is shown to reflect the automatic activation of lexical representations (Forster et al. 2003), whereas subliminal semantic activation may yield no or only minor changes in behavioral measures (Damian 2001; Kouider and Dupoux 2004; Kouider and Dehaene 2007). Indeed, neuropsychological and brain imaging studies converge to suggest that amodal semantic knowledge is represented broadly in the anterolateral temporal cortex that is distinct from the MTG and FG (Chertkow et al. 1997; Hillis et al. 2001; Martin and Chao 2001; Levy et al. 2004). Conversely, the MTG may be involved in lexical activation since the adjacent posterior temporal region is shown to exhibit increasingly greater response as a set of local letter combinations become more like real words (Vinckier et al. 2007).

Neural Effects of Within- and Cross-language Priming

In turn, repetition suppression at the left FG should be attributed to prelexical stages of reading because this region exhibited no cross-language effects irrespective of translation directions. Yet, the same region was sensitive to size-invariant features of language-specific orthographies since it exhibited repetition suppression in each language. This language sensitivity is also supported by the observed changes in bottom-up FG-IFG coupling as a function of target language (see Fig. 3). These findings are generally consistent with the notion that the left FG is associated with abstract orthographic codes at the prelexical level (Cohen et al. 2002). It is of note, however, that this prelexical component plays a minor role in the generation of behavioral priming effects (Forster et al. 2003).

We found that L1 and L2 exhibit the same pattern of within-language priming along the left occipitotemporal cortex including the FG and MTG. Given the bottom-up nature of unconscious priming (Naccache and Dehaene 2001), this finding suggests that the FG-MTG stream constitutes an autonomous and language-nonspecific component of bilingual word recognition, which probably mediates lexical activation in each language, as argued above. Indeed, the coupling strength between FG and MTG did not change with target language despite the gross between-language activation differences in conscious word processing (see Table 1 and Fig. 3). Importantly, however, unconscious occipitotemporal activation by masked primes may be bound with language membership and not spread across different languages because our fMRI results revealed that neural priming in the medial fusiform region is in fact tagged with language identity. This finding is in good accord with a bilingual word recognition model positing that such language tags serve as a local inhibitory mechanism for deactivating nontarget language (Dijkstra and Van Heuven 2002). Thus, the language-nonspecific FG-MTG stream probably mediates lexical activation in each language but not cross-language lexical activation or semantic activation.

We further identified the left MTG as a neuroanatomical substrate of masked cross-language priming that is known to be asymmetric between translation directions at the behavioral level. Given that the neurocognitive processes driven by subliminal primes are language sensitive and modular as argued before, we propose that the observed priming at the MTG should be attributed to asymmetric cross-language lexical activation in conscious word processing. Here, a key assumption is that lexical codes in L2 are connected to their translation equivalents in L1 more strongly than in the reverse direction (Kroll and Tokowicz 2001). Given this asymmetric lexical connection model and our observations, the net effect of L1-L2 priming can be interpreted as indicating that the conscious recognition of L2 targets benefit from evidence accumulation in the L1 lexical system, which is preactivated by L1 primes and further amplified by L2 targets via strong lexical-level connections from L2 to L1. For the L2-L1 direction, however, such cross-language facilitation would not occur because masked L2 primes can induce covert activation only in the L2 lexical system (see before), which cannot contribute to the conscious recognition of L1 targets because of the much weaker lexical connections from L1 to L2.

Strategic Control in Conscious Language Recognition

Between-trial changes of visible target language produced an enhanced response at the MTG ($\gamma = -45$). The analyses of effective connectivity revealed that upon switching, this same region received a crossover, language-specific modulatory influence only from the IFG, suggesting that the switch-related response at the MTG was elicited by top-down signals, rather than by stimulus-driven activation in occipitotemporal cortex. Our TMS results further showed that such top-down, reentrant signals from posteroinferior frontal cortex play a causal role in bilingual language control since the conscious switch to L2 was disrupted by the stimulation of the IFG and not by the stimulation of the posterior MTG involved in earlier, bottom-up stages of reading. Thus, these findings demonstrate that the IFG-MTG circuitry is functionally distinct from the visual word-form system in occipitotemporal cortex and operates for language control in a later stage of word recognition even when

no overt articulatory response is required. In turn, the IFG may exert reactive control during language switch by receiving bottom-up signals specifying language membership since the early neural component in the left FG is already sensitive to the type of input language before lexical activation (see Fig. 3).

More specifically, we propose that the observed cross-language asymmetry in top-down modulation reflects a strategic amplification of a weaker language during postlexical stages of reading. First, our behavioral and fMRI results suggest that the bottom-up activation of lexical codes, be it L1 or L2, can be completed equally in the upstream occipitotemporal cortex, including the FG and MTG (see above). This in turn implies that the top-down modulation of the MTG reflects lexical or some later stages of word processing. Consistently, recent lesion analyses of brain-damaged patients show that the MTG and adjacent lateral temporal regions are involved in a postlexical process for mapping word form onto word meaning (Dronkers et al. 2004; Vandenbulcke et al. 2007; Campanella et al. 2009).

Second, there is a body of behavioral evidence suggesting that L2 words are connected to the conceptual system only weakly relative to L1 words (Kroll and Tokowicz 2001). Thus, an additional strategic amplification of the weaker lexicosemantic link should be required for yielding a behavioral response in L2 during semantic categorization. Indeed, recent brain imaging work points to the existence of a general purpose cognitive control system in inferolateral prefrontal cortex, which resolves conflict by enhancing neural representations of task-relevant information in posterior temporal cortex (Egner and Hirsch 2005). Taken together, these observations suggest that the postlexical mapping of word-form to meaning in the left MTG is much less automatic for L2, which is later compensated by an effortful cognitive control for amplifying the lexicosemantic association specific to each language.

Conclusions

We found a double dissociation between the autonomous and strategic components of the bilingual reading system. The observed switch of the IFG-MTG reflects a strategic reconfiguration of language-specific task schema and overcomes the bottleneck in L2 recognition by amplifying the lexicosemantic association in posterior temporal cortex. Our results therefore point to a neurocognitive locus of the nonplastic language dominance observed even with highly proficient bilinguals. The cognitive delay in L2 reflects the strategic process to enhance task-relevant lexicosemantic knowledge in the nondominant language, rather than a weaker processing power of the visual word recognition system.

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