

Stimulus-driven changes in the direction of neural priming during visual word recognition



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ABSTRACT

Visual object recognition is generally known to be facilitated when targets are preceded by the same or relevant stimuli. For written words, however, the beneficial effect of priming can be reversed when primes and targets share initial syllables (e.g., “boca” and “bono”). Using fMRI, the present study explored neuroanatomical correlates of this negative syllabic priming. In each trial, participants made semantic judgment about a centrally presented target, which was preceded by a masked prime flashed either to the left or right visual field. We observed that the inhibitory priming during reading was associated with a left-lateralized effect of repetition enhancement in the inferior frontal gyrus (IFG), rather than repetition suppression in the ventral visual region previously associated with facilitatory behavioral priming. We further performed a second fMRI experiment using a classical whole-word repetition priming paradigm with the same hemifield procedure and task instruction, and obtained well-known effects of repetition suppression in the left occipito-temporal cortex. These results therefore suggest that the left IFG constitutes a fast word processing system distinct from the posterior visual word-form system and that the directions of repetition effects can change with intrinsic properties of stimuli even when participants' cognitive and attentional states are kept constant.

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Introduction

As a general rule, vocabulary size of a language exceeds by far the number of letters used in the same language. In English, for example, more than 300,000 entries in a standard dictionary (<http://www.oed.com/>) are written with only 26 alphabet letters. This fact naturally suggests that many similar combinations of letters should co-exist as different words in almost any written language in the world. An important step for fluent reading is therefore fast and effective analysis of letter-strings for distinguishing a word (e.g., “spice”) from other, visually similar “neighbor” words (e.g., “spite”, “space”, “slice”, “spike” and so on). This early stage of word processing is often challenging for non-skilled readers, such as children and dyslexics (Goulandris, 2006) and can be also a common source of reading errors even for fully literate adults (Grainger et al., 1992). In fact, previous behavioral studies have shown that orthographic similarity of letter-strings strongly influences participants' behavioral response to written words. For instance, visual recognition of a target word (e.g., “diva”) is known to be accelerated when it is preceded by a pseudoword prime sharing the same consonant structure (e.g., “duva”) (New et al., 2008).

Interestingly, however, it is also known that prime–target orthographic overlap can produce an opposite pattern of behavioral effects

in other circumstances. That is, unlike the facilitatory effect of consonantal priming produced by pseudoword primes (New et al., 2008), behavioral response to targets (e.g., “char”) is known to be slowed down when they are preceded by real word primes having shared initial segments (e.g., “chat”) than when preceded by primes without such sublexical overlap. Similar inhibitory modulation of visual word processing seems to occur across different languages when prime and target share a set of initial letters (De Moor et al., 2007; Segui and Grainger, 1990) or a first syllable (Carreiras and Perea, 2002; Mathey et al., 2006; Nakamura et al., 2012a; Nakayama et al., 2011). This negative effect of neighbor priming, occurring only for real word primes, has been thought to arise from a word-level lateral inhibition mechanism, whereby orthographically overlapping primes activate multiple lexical codes which would compete and interfere with targets during visual word recognition (Grainger and Jacobs, 1996). Such lateral inhibition among orthographic neighbors seems to be greater in the left hemisphere than in the right hemisphere, since some previous studies show that orthographic neighbors flashed to the right visual hemifield (RVF) produce greater inhibitory effects relative to those to the left visual hemifield (LVF) (Nakamura et al., 2012a; Perea et al., 2008). The possible hemispheric difference in inhibitory effects may reflect the well-known left-hemisphere advantage in fine-grained analysis of local visual features (Beeman et al., 1994; Ivry and Robertson, 1998).

Indeed, several event-related potential (ERP) studies have shown that neural response associated with those inhibitory effects appears at 250–350 ms after target onset and tends to be lateralized to the

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left-hemisphere (Friedrich, 2005; Friedrich et al., 2013; Massol et al., 2010). To date, however, little is known about specific neuroanatomical structures involved in inhibitory priming during reading. It is nonetheless possible to predict some candidate brain regions from the lexical competition hypothesis as described above. That is, while lateral inhibition among lexical neighbors is thought to be the main source of negative priming effects, lexical activation in itself should rely on bottom-up signals from sublexical levels, either orthographic or phonological (Alvarez et al., 2004; Carreiras and Perea, 2002; Segui and Grainger, 1990). Thus, it is likely that cognitive loci of syllabic priming encompass lexical, orthographic and phonological codes of written words. At the neural level, previous brain imaging studies have identified neural correlates of lexico-semantic memory in the left lateral temporal cortex (LTC) (Campanella et al., 2009; Vandenbulcke et al., 2007). This region is located downstream of the left posterior occipito-temporal sulcus (pOTS) involved in abstract orthographic codes of written words (Dehaene et al., 2005) and seems to play a multimodal role in word processing (Chertkow et al., 1997; Cohen et al., 2004; Vandenberghe et al., 1996). On the other hand, phonological computation of words is known to be a fast and robust cognitive component of fluent reading (Frost, 2003) and thus may play a role in the generation of masked syllabic priming. Recent brain imaging data suggest that such rapid activation of phonological codes is mediated by the left inferior frontal area involved in speech production (Cornelissen et al., 2009; Klein et al., 2015; Pammer et al., 2004; Wheat et al., 2010).

In addition, it is also possible that the inhibitory effects arise at later processing stages involved in behavioral response, such as decision

masking and motor planning, because most of the effects reported seem to appear only during categorical judgment tasks and not during other language tasks without decision making (e.g., word naming) (Carreiras et al., 2005; Schiller, 2004; You et al., 2012). Such motor response stage of word processing has been thought to rely on the premotor region involved in motor preparation and execution (Nakamura et al., 2007; Rissman et al., 2003).

Using functional magnetic resonance imaging (fMRI), the present study investigated how these neural components contribute to the generation of inhibitory priming (Experiment 1). In each trial, participants made natural/artificial judgment about a centrally presented target, which was preceded by a masked prime flashed either to the left or right visual field (Fig. 1A). Consistent with previous behavioral studies, participants responded more slowly when primes and targets shared initial syllables than when not. This behavioral effect of syllabic priming was independent of motor response bias during semantic judgment (see *Methods* section). At the neural level, we observed that the effect of inhibitory priming was associated with a robust effect of repetition enhancement in the left inferior frontal gyrus (IFG). On the other hand, the left dorsal premotor area (PMd) and LTC, although showing activation increase associated with motor response, exhibited no significant priming associated with syllabic overlap.

Therefore, the observed neural priming in the left IFG clearly differed from repetition suppression in the pOTS and its adjacent regions that has been associated with facilitatory behavioral priming during visual word recognition (Dehaene et al., 2005). In fact, however, it is known that behavioral priming can depart from repetition suppression

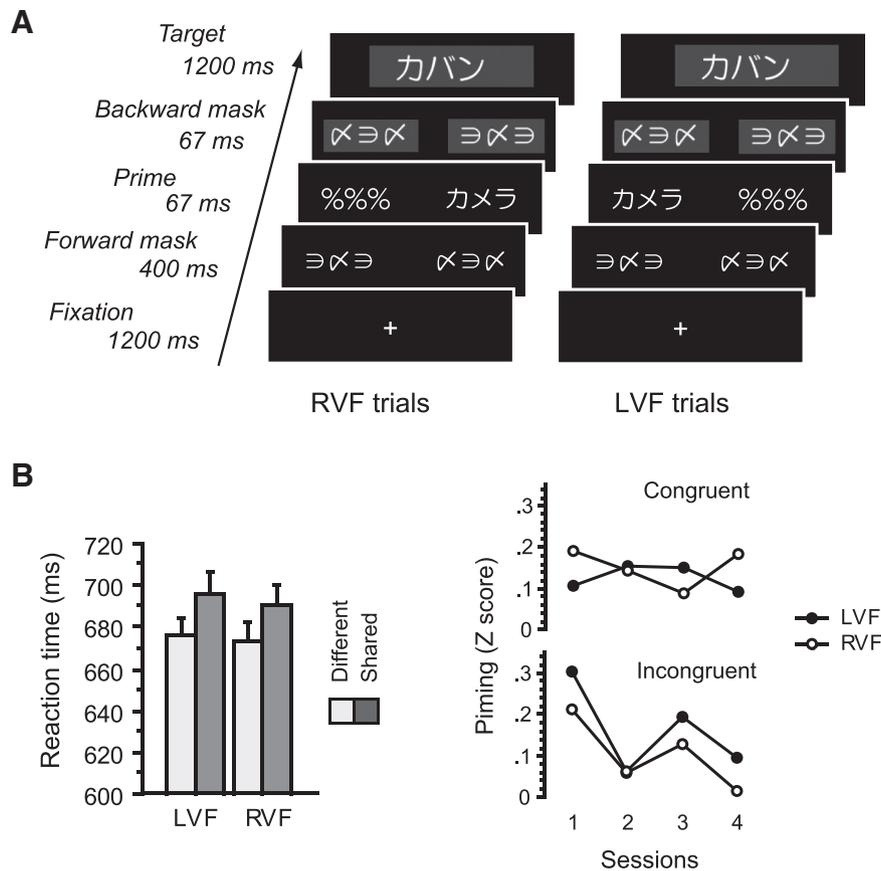


Fig. 1. Experimental paradigm and behavioral data for Experiment 1. (A) Each trial consisted of a forward mask, a prime and a visual foil, a backward masks and a target. We manipulated the visual hemifield of masked primes (LVF or RVF) and prime–target syllabic overlap at word-onset (shared or different). Primes and targets belonged either to the same category or to different categories. Participants made natural/artificial judgment by key-press with their right index and middle fingers. (B) Mean reaction time during semantic categorization (left) and temporal evolution of priming effects (in Z score units) separated by response congruency (right). Participants responded more slowly when primes and targets shared the same syllables at word onset than when they did not. The overall effect-size of this negative priming did not differ between the two hemifields. However, when restricted to congruent trials, the magnitude of syllabic priming tended to be larger in RVF trials than in LVF trials during the first session (see *Results* section).

(e.g., Sayres and Grill-Spector, 2006) and may occur with enhancement, particularly in prefrontal areas (Grill-Spector et al., 2006; Henson and Rugg, 2003; Schacter et al., 2004). More specifically, repetition effects in fMRI seem to be biased toward enhancement depending on several different cognitive mechanisms, such as stimulus recognition, learning, attentional states, expectation and explicit memory (see Segaert et al., 2013 for a recent review). It is also important to note that repetition effects may vary across brain regions and thus can appear differently between prefrontal and posterior temporal regions (Verhoef et al., 2008).

We therefore performed an additional fMRI experiment with a more typical repetition priming paradigm in which prime and target were either the same word or unrelated words at the whole word level (Experiment 2). This second experiment was motivated because we wanted to confirm that the effect of repetition enhancement obtained from Experiment 1 indeed arose from syllabic overlap itself, rather than other experimental factors associated with the divided hemifield presentation procedure. This latter possibility should be ruled out, since rapid and unpredictable changes of the prime hemifield might influence the cognitive or attentional state of participants, which in turn could reverse the directions of fMRI priming (Henson and Rugg, 2003; Segaert et al., 2013). If these endogenous factors associated with the behavioral paradigm, then it is expected that typical repetition suppression should emerge when primes and targets were overlapping at the word-level.

Methods

Participants

A total of twenty-one healthy volunteers participated in the present study, including 12 participants (one female, age-range 19–41 years, mean 24.1 years) for Experiment 1 and 10 participants (one female, age-range 20–27 years, mean 21.8 years) for Experiment 2. None of them received both experiments. All of them were right-handed, native speakers of Japanese and undergraduate or postgraduate students at Kyoto University. None of them had known neurological or psychiatric disorders. All had normal or corrected-to-normal vision and gave written informed consent prior to the experiments. One participant in Experiment 2 was excluded from behavioral and brain imaging analyses because of excessive head motion (>2.4 mm). The protocol of this study was approved by the ethical committee of the Graduate School of Medicine, Kyoto University.

Behavioral paradigm

For Experiment 1, we selected 30 Japanese nouns (mean log frequency (SD) = 1.02 (0.45) per million) written with three or four characters in katakana script (a Japanese syllabary comprising 48 characters and diacritic marks). All of these words were high in visual familiarity, with their mean familiarity level (SD) being 5.99 (0.79) on the 1–7 scale in the NTT database (Amano and Kondo, 2000). Half of them represented natural objects and the other half artificial objects. These words were used as primes (e.g., /ka-me-ra/, “camera”) and coupled either with target words sharing onset syllables (e.g., /ka-ba-n/, “bag”) or those without such syllabic overlap at the word-onset (e.g., /bi-de-o/, “video”). Primes and targets also belonged either to the same category or to different categories, thus giving 120 prime–target pairs. Lexical frequency and visual familiarity of targets were matched to those of primes (0.85 (0.48) per million and 6.10 (0.33), respectively). Each trial consisted of central fixation (1200 ms), a forward mask (400 ms), a masked prime and a visual foil (“%%”, ~3.5° in visual length, 67 ms), a backward mask (67 ms) and a centrally-presented target (~4.5°, 1200 ms) (Fig. 1A). The masks were a string of character-like symbols (“α ∩ α” and “∩ α ∩”) assigned pseudo-randomly either to the left or right visual fields (LVF and RVF). Masked primes and visual foils were flashed either to LVF or RVF with a probability of 50%. In each trial,

participants decided as quickly and accurately as possible whether targets represented natural or artificial objects by pressing keys with their right index or middle fingers. We previously showed that, although healthy young participants are partially aware of masked primes under the same procedure, the magnitude of priming does not change significantly with the perceptual discriminability of primes (Nakamura et al., 2012a). We also included trials with only masked primes without targets to measure the extent of cerebral activation produced by masked words in each hemifield. Each participant received four sessions, each consisting of 240 trials (~25 trials per condition and 40 word-absent baseline trials per session). Due to a technical error, behavioral response data from two participants were partially unavailable and thus were excluded from error analysis.

For Experiment 2, we prepared a separate set of 110 prime–target pairs. Lexical frequency and visual familiarity of targets were matched with those of words used in Experiment 1 (0.85 (0.49) per million and 6.09 (0.33), respectively). Prime words were either identical as target words or different words without syllabic overlap at their initial segments. Participants made semantic judgment about target words presented in the same sequence of stimuli as Experiment 1. In this second experiment, however, primes and targets always belonged to the same category and thus yielded no response incongruity between primes and targets. This is because (1) our main goal was to verify the priming directions of the IFG and POTS during the classical repetition priming task and (2) we observed in Experiment 1 that the effect of repetition priming in these regions did not differ between congruent and incongruent trials. Each participant received four sessions, each consisting of 180 trials (~36 trials per condition per session).

Imaging procedure

Imaging data were acquired using a Siemens Trio 3 T head scanner with a standard head coil optimized for echo-planar imaging sequence (22 contiguous slices, 4 mm thickness with 1 mm gap, repetition time = 1400 ms, echo time = 30 ms, flip angle = 90°, field-of-view = 256 × 256 mm², 64 × 64 pixels). High-resolution T1 anatomical scans were performed after each experiment. Participants in Experiment 1 received four scanning sessions, each lasting ~710 s, while those in Experiment 2 had three sessions, each lasting ~540 s.

Data analysis

Imaging data were preprocessed and analyzed using the Statistical Parametric Mapping (SPM8) package software (<http://www.fil.ion.ucl.ac.uk/spm/>). Functional images were corrected for head movement and slice timing, normalized to the standard brain space by the Montreal Neurological Institute (MNI) and smoothed with an isotropic Gaussian kernel (full-width at half-maximum = 5 mm). For Experiment 1, we constructed a general linear model including four types of trials (i.e., 2 × 2 factorial for levels of prime hemifield and syllabic overlap) and two additional types for “prime only” trials (LVF and RVF). For each participant, condition-specific contrast images for these six effects were calculated relative to the baseline by convolving known time-series of trials with a canonical hemodynamic response function and its time derivative. These contrast images were submitted to the second-level analysis using one-way analysis of variance (ANOVA). Repetition suppression and enhancement were calculated as decrease and increase of activation in “shared syllable” trials relative to “different syllable” trials, respectively. Unless stated otherwise, all effects of interest were tested with voxel-level $p < 0.001$ and cluster-level $p < 0.05$ corrected for the whole brain volume. To assess the effects of priming in the language network more closely, we further used probabilistic functional maps (Fedorenko et al., 2010) to examine three regions of interest (ROIs) previously associated with language processing, i.e., the left IFG (peak coordinates = −48, 16, 24) involved in speech production, left LTC (−56, −40, 10) associated with lexical memory

(Campanella et al., 2009; Vandenbulcke et al., 2007) and posterior superior temporal gyrus (pSTG; $-48, -62, 15$) involved in speech perception (Lee et al., 2014). We also created two 5-mm radius spherical ROIs, one centered at $-40, -50, -14$ in the left pOTS corresponding to the “visual word-form area” (Dehaene et al., 2010b) and the other centered at $-38, -4, 58$ in the left PMd involved in the execution and preparation of hand movements (Mayka et al., 2006). Statistical significance was examined with voxel $p < 0.05$ corrected for multiple comparisons across the search volume.

In addition, since primes and targets belonged to different categories in half of trials (see above), we examined possible effects of prime–target response congruency (Eimer and Schlaghecken, 1998) using a separate model which included prime hemifield (LVF and RVF), prime–target response congruency (congruent and incongruent) as within-participants factors. This is important because (1) masked primes can prepare participants' response before target processing, such that response conflict occurs when primes and targets belong to different categories but not when they are from the same category, and (2) such response congruency effects can influence priming patterns at both behavioral and neural levels (Abrams et al., 2002; Dobbins et al., 2004).

For Experiment 2, we computed condition-specific contrast images relative to the baseline for the four event types (prime hemifield \times prime–target identity) for each participant, and then submitted these images to the second-level ANOVA. In final between-groups analysis, we examined the magnitude of priming between the two experiments by pooling four contrast images (same-LVF, different-LVF, same-RVF and different-RVF trials, each contrasted with the word-absent baseline) from each of the 21 participants. This joint analysis was made for each ROI using a $2 \times 2 \times 2$ ANOVA which included the effects of hemifield (LVF and RVF) and prime–target identity (same and different) as within-participant factors and the unit of overlap (syllable and whole word) as a between-participants factor.

Results

Experiment 1

Behavioral results

Participants performed the semantic categorization task with only few errors (mean error rate (SD) = 5.99 (5.25) %). Median reaction times for correct responses (Fig. 1B) were examined using a 2×2 ANOVA with the visual hemifield (LVF and RVF) and syllabic overlap (same and different) as within-participant factors. Participants overall responded 19 ms more slowly when primes and targets shared onset syllables than when otherwise ($p < 0.005$), whereas response latency did not differ between LVF and RVF trials ($p > 0.2$). The interaction between syllabic overlap and prime hemifield was not significant ($p > 0.1$), suggesting that the magnitude of syllabic priming did not differ between LVF trials and RVF trials.

We then assessed the possible contribution of prime–target semantic congruency in the observed effect of inhibitory priming. That is, the effect of syllabic overlap might be partially attributed to prime–target response congruency, since primes and targets belonged to different semantic categories in half of trials (see Methods section). We ran a separate $2 \times 2 \times 2$ ANOVA which included the visual hemifield (LVF and RVF), syllabic overlap (same and different) and prime–target congruency (congruent and incongruent) as within-participant factors. Participants responded 9 ms faster in congruent trials than in incongruent trials, but this effect of congruency did not reach significance ($p = 0.11$). Next, the magnitude of syllabic priming was 16 ms in congruent trials and 21 ms in incongruent trials, and this difference was also non-significant ($p > 0.5$). Thus, these results suggest that the effect of negative syllabic priming did not change with response congruency.

In Fig. 1B, we further examined the temporal evolution of syllabic priming effects with respect to response congruency. This was

motivated because such response bias associated with prime–target semantic congruency is known to increase over time via a learned stimulus–response association and change the patterns of priming (Dobbins et al., 2004). To reduce large inter-session variability for each participant, we transformed reaction time data from four scanning sessions into Z scores such that each participant had a mean of zero (e.g., Frost, 2003; Ziegler et al., 2014), and computed the magnitude of syllabic priming for each priming condition for each session. This priming index was then examined with a 2×2 analysis of covariance (ANCOVA) which included the visual hemifield (LVF and RVF) and response congruency (congruent and incongruent) as main effects and the number of session as a covariate. This analysis revealed a significant effect of session ($p = 0.03$), suggesting that the magnitude of priming indeed changed over time. Indeed, the effects of syllabic priming appeared differently between congruent and incongruent trials in earlier stages of the experiment (see Fig. 1B). In particular, when the analysis was restricted to the first scanning session, the effect of syllabic priming for congruent trials was greater for RVF than for LVF (20 ms vs. 7 ms) whereas this left–right difference approached significance ($p < 0.08$). These findings may account for the symmetrical syllabic priming observed in the present study, which seems to be at odds with the previously known left-hemisphere dominance in inhibitory regulation over lexical neighbors (Nakamura et al., 2012a; Perea et al., 2008).

Imaging results

The semantic categorization task strongly activated the bilateral occipito-temporal and prefrontal cortices relative to the word-absent baseline. We first looked at the extent of cerebral activation in prime-only trials relative to the baseline, but found no significant activation (voxel $p > 0.01$, uncorrected). When compared between prime hemifields, no significant activation difference was observed between LVF primes and RVF primes throughout the entire brain volume ($p > 0.01$).

Next, to identify brain regions associated with the behavioral syllabic priming effects observed above, we searched for brain regions showing the main effect of repetition suppression induced by the syllabic overlap between primes and targets (i.e., activation reduction in shared trials relative to different trials). However, no brain region emerged as significant, even when the statistical threshold was lowered to a more lenient level at uncorrected voxel-level $p < 0.01$ (cluster extent > 10 voxels). We then searched for brain regions showing the opposite direction of priming, “repetition enhancement” induced by shared syllables. This contrast revealed a robust effect of enhancement in the left inferolateral frontal cortex (1168 voxels, Fig. 2A), including the local maximum in the anterior IFG ($-46, 28, 20, Z = 4.19$) and two subpeaks in the posterior IFG ($-42, 12, 20, Z = 3.93$) and inferior frontal sulcus ($-36, 0, 24, Z = 3.89$). Additional analyses for left frontal ROIs (Fedorenko et al., 2010) revealed a significant effect of repetition enhancement in the pars orbitalis of the left IFG ($-34, 28, 10, p < 0.02$) but not in the left middle frontal gyrus ($p > 0.1$). In the same prefrontal area, the magnitude of repetition enhancement tended to be greater in RVF trials than in LVF trials (Fig. 2B), although this difference did not reach statistical significance ($p > 0.1$).

In Fig. 2B, we further examined the same effect by restricting the search volume to five a-priori defined ROIs previously associated with word processing (see Methods section). Consistent with the whole brain SPM, the left IFG showed a significant effect of repetition enhancement ($p = 0.003$). The same effect of enhancement was also found at the pOTS ($p < 0.05, -44, -50, -12$), although this region did not emerge in the whole-brain analysis. The effect of repetition enhancement was non-significant in other regions ($p > 0.1$ for all).

For the IFG and pOTS, we plotted the temporal evolution of repetition enhancement effects in Fig. 2C. This is because the number of stimulus presentation might be a key determinant for the directions of fMRI priming effects (Muller et al., 2013; Reber et al., 2004). For the left IFG, however, the direction of priming was already pronounced in the first

session and remained constant through the subsequent sessions. For each region, the magnitude of repetition enhancement was then submitted to a one-way ANCOVA treating the prime hemifield (LVF and RVF) as a factor and the session as a covariate. We confirmed that these effects and their interaction were all non-significant in the left IFG ($p > 0.4$ for all), whereas this was also the case for the left pOTS ($p > 0.14$ for all).

We then analyzed the effects of response-congruency priming using a separate $2 \times 2 \times 2$ ANOVA with prime hemifield (LVF and RVF),

syllabic overlap (same and different) and prime–target congruency (congruent and incongruent) as within-participant factors. We initially looked for voxels activated by congruent trials relative to incongruent trials, but found no significant region at the stringent whole-volume statistical threshold. However, at a more lenient threshold ($p < 0.001$, uncorrected), the effect of congruency was found in the left middle temporal gyrus ($-58, -42, 8$; 178 voxels, $Z = 3.61$). In ROI analyses (Fig. 3A), this effect was significant at the left LTC ($p = 0.03$) and left PMd ($p < 0.04$) and observed as a weaker trend in the left pOTS ($p = 0.06$). Other regions were all non-significant ($p > 0.1$). In contrast, no brain region showed greater activation in incongruent trials than in congruent trials (uncorrected voxel $p > 0.01$).

For these regions, we additionally plotted the temporal evolution of this congruency priming in Fig. 3B. It was seen that the effect of response congruency at the PMd was almost absent at the start of the experiment and gradually increased over time. This increasing trend in congruency priming was confirmed by a one-way ANCOVA with the prime hemifield (LVF and RVF) as a within-participant factor and the session as a covariate, which showed a significant effect of session ($p < 0.05$). By contrast, these effects and their interaction were non-significant in the LTC ($p > 0.9$ for all). This finding is also in good accord with the notion that such congruency priming arises from a learned association between stimulus and response when same stimulus items are repeated multiple times (Dobbins et al., 2004).

Experiment 2

Behavioral results

Participants again performed the categorization task with high accuracy (mean error rate (SD) = 4.20 (1.56) %). Median reaction times for correct responses (Fig. 4A) were examined with a 2×2 ANOVA with the prime hemifield (LVF and RVF) and word identity (same and different) as within-subject factors. We observed a significant facilitatory effect of repetition priming ($p < 0.05$), suggesting that participants responded faster when primes and targets were identical than when otherwise. The effect of hemifield and its interaction with repetition were both non-significant ($p > 0.1$).

We then looked at the temporal evolution of priming effects and observed that the direction of repetition priming was overall positive and consistent across sessions (Fig. 4A). Like in Experiment 1, we also computed the priming index for each session and assessed the temporal evolution of priming effects using a one-way ANCOVA with the prime hemifield (LVF and RVF) as a factor and the session as a covariate. The effects of hemifield and session and their interaction were all non-significant ($p > 0.2$ for all).

Next, we compared the reaction time data between the two experiments using a $2 \times 2 \times 2$ ANOVA with the effects of hemifield and prime–target identity as within-participant factors and the unit of overlap (syllable and whole word) as a between-participants factor. Overall reaction time differed neither between Experiments 1 and 2 (689 ms vs. 684 ms, $p > 0.9$) nor between LVF and RVF (686 ms vs. 685 ms,

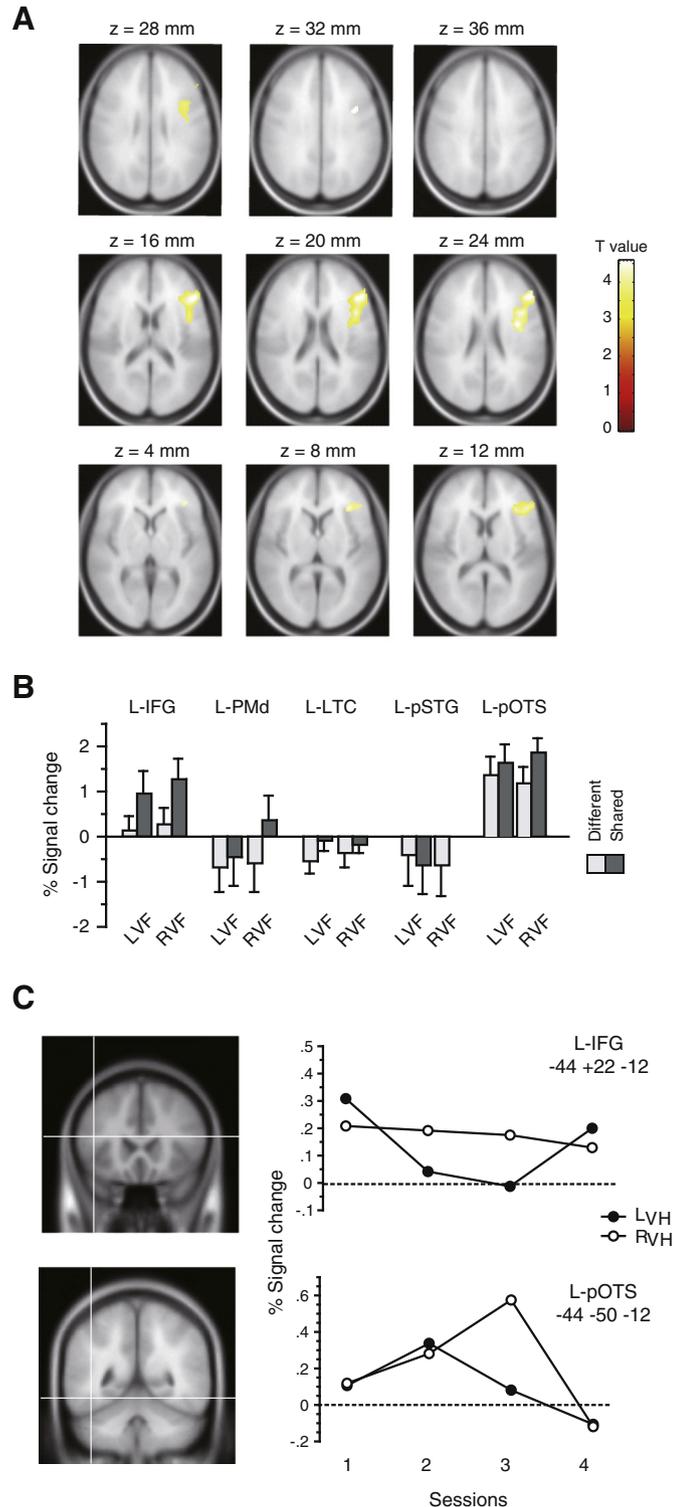


Fig. 2. fMRI results in Experiment 1. (A) Repetition enhancement associated with inhibitory syllabic priming. In the whole-brain analysis, only the left IFG ($-46, 28, 20$, $Z = 4.19$) emerged as showing a robust effect of repetition enhancement. This left inferiorlateral prefrontal cluster extended to the posterior IFG ($-42, 12, 20$, $Z = 3.93$) and inferior frontal sulcus ($-36, 0, 24$, $Z = 3.89$). Repetition enhancement was also observed in the pars orbitalis ($-34, 28, 10$) but not in the left middle frontal gyrus (see Results section). In contrast, no brain regions exhibited significant effects of repetition suppression. (B) Activation profiles at five ROIs previously associated with word processing. For each region, percent signal change relative to the baseline is plotted at the most significant voxel for each trial type. The left IFG and pOTS both exhibited significant effects of repetition enhancement. For the IFG, this priming effect tended to be greater for RVF relative to LVF ($p = 0.002$, uncorrected, but see Results section). Other regions also showed no significant left–right difference between the two hemifields. (C) Temporal evolution of priming effects in the left IFG and pOTS. The magnitude of priming is plotted against the number of scanning sessions (positive and negative effects each represent enhancement and suppression). Note that the left IFG already exhibited repetition enhancement in the first session, whereas this effect remained constant through the subsequent sessions.

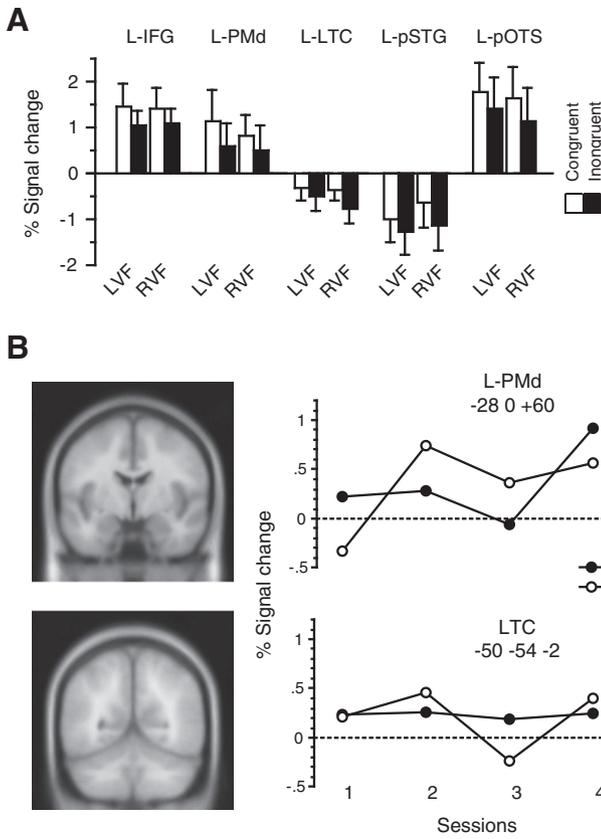


Fig. 3. Effects of response congruency in Experiment 1. (A) Activation profiles at the five ROIs. The effect of response congruency priming, i.e., activation reduction in congruent trials relative to incongruent trials, was significant at the left PMd and pOTS. The same trend was also observed at the left LTC (see Results section). (B) Temporal evolution of congruency priming in the left PMd and LTC. The effect of response congruency showed an increasing trend at the PMd but remained almost constant at the LTC.

$p > 0.9$). The effect of identity was significant, with different trials being responded to 9 ms faster than shared trials ($p < 0.03$). Importantly, however, there was significant cross-over interaction between identity and overlap ($p = 0.002$), validating the finding that the patterns of priming shifted between the two experiments. Other interactions were all non-significant ($p > 0.1$).

Imaging results

The semantic categorization task again activated the bilateral occipito-temporal and prefrontal cortices relative to the baseline. We searched for brain regions showing the main effect of repetition suppression, but no region emerged as significant. Yet this is likely because of the small sample size of this additional experiment. Indeed, ROI analyses in Fig. 4B revealed that the effect of repetition suppression was significant at the pOTS ($p < 0.02$), thus replicating the classical pattern of repetition priming during visual word recognition. This same effect was non-significant for all other ROIs ($p > 0.1$ for all). In the left pOTS, the magnitude of repetition priming did not differ between LVF and RVF trials in the same area (uncorrected $p > 0.01$). As shown in Fig. 4C, this region exhibited a consistent pattern of neural priming across the three sessions. Indeed, one-way ANCOVA revealed no significant effect of session on the magnitude of repetition suppression ($p > 0.16$). Repetition enhancement was not detected throughout the whole brain volume, even when a more lenient threshold was applied (uncorrected $p > 0.01$).

Lastly, we compared the magnitude of priming between the two experiments by pooling four contrast images (same-LVF, different-LVF, same-RVF and different-RVF trials, each contrasted with the word-

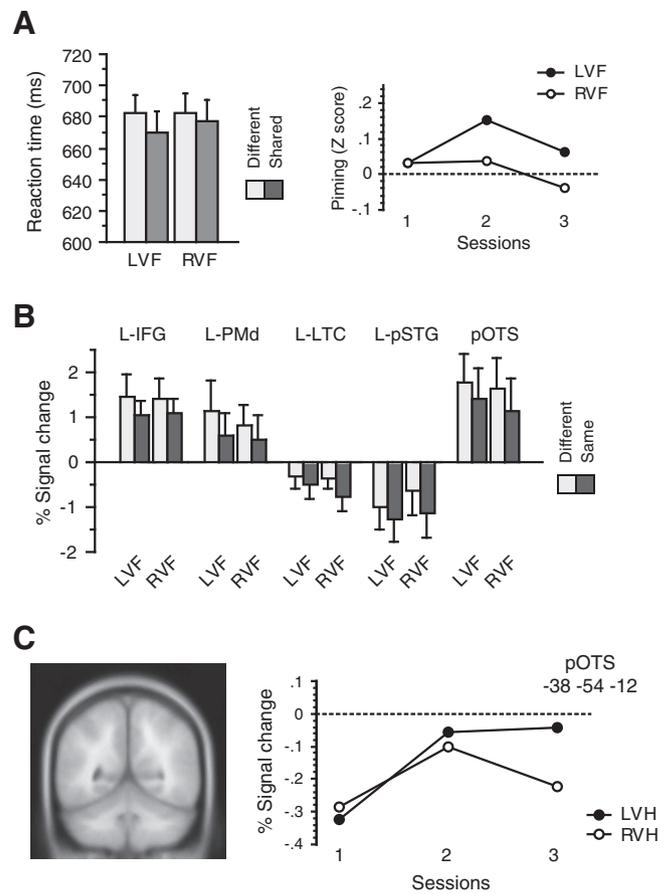


Fig. 4. Behavioral and fMRI results in Experiment 2. (A) Mean reaction time during semantic categorization (left) and temporal evolution of priming effects (in Z score units) (right). Participants responded faster when primes and targets were the same words than when otherwise, while the magnitude of this facilitatory priming did not differ between the two hemifields. The direction of repetition priming was overall positive and consistent across sessions, except the negative effect observed for LVF trials during the first session. (B) Activation profiles at the five ROIs. The left pOTS showed the well-known pattern of repetition suppression, irrespective of the prime hemifield. The left IFG, PMd and LTC also showed the similar trend of repetition-related activation reduction, but these effects did not approach significance (see Results section). (C) Temporal evolution of repetition priming in the left pOTS. This region showed a consistent trend of repetition suppression through the three sessions.

absent baseline) from each of the 21 participants. In parallel with the behavioral analysis, this between-experiments comparison was made for each ROI using a $2 \times 2 \times 2$ ANOVA which included the effects of hemifield (LVF and RVF) and prime-target identity (same and different) as within-participant factors and the unit of overlap (syllable and whole word) as a between-participants factor. As for the pOTS, the effect of prime-target identity was observed as repetition enhancement in Experiment 1 and repetition suppression in Experiment 2, respectively, as described above. In the present joint analysis, this change in priming directions was confirmed as a significant cross-over interaction between identity and unit in the same area ($-38, -52, -10, p = 0.001$). The similar trend of cross-over interaction between identity and overlap was also observed at the left IFG ($-50, 34, 24, p < 0.07$). However, no other regions showed a trend of between-experiments difference ($p > 0.1$).

Discussion

The present behavioral results from Experiment 1 replicated the well-known pattern of inhibitory priming during visual word recognition (Carreiras and Perea, 2002; Carreiras et al., 1997; Davis and

Lupker, 2006; Pollatsek et al., 1999). This negative priming has been thought to reflect lateral inhibition of lexical competitors during orthographic or phonological processing of written words, which might be strongly associated with the left hemisphere reading system (Friedrich, 2005; Friedrich et al., 2013; Nakamura et al., 2012a; Perea et al., 2008). Therefore, we initially expected that the magnitude of this syllabic priming would be greater in RVF trials than in LVF trials, but obtained only a trend of hemispheric asymmetry during the first scanning session even when the confounding effect of response congruency was discounted. This finding might be partially attributed to a rapid learning of task-relevant information during scanning sessions, which is likely to develop over repeated exposure to the same stimuli and transfer between the left and right hemispheres (e.g., Lapierre et al., 2013; Pavlovskaya and Hochstein, 2011).

It is important to note that participants might be partially aware of prime stimuli because the duration of primes in the present study was slightly longer than the one used in typical subliminal priming studies (Kouider and Dehaene, 2007). In this sense, it is still open whether the effect of inhibitory priming can occur when participants are strictly unconscious of primes, since most previous studies of orthographic or syllabic priming have used prime durations of >50 ms, which probably produce “partial awareness” of stimulus identity (Kouider and Dehaene, 2007). However, phonological computation has been shown to be a highly automatic component of reading and run in a bottom-up fashion irrespective of participants’ strategic control (Frost, 2003). Indeed, the inhibitory effects of syllabic neighbors seem to be largely independent of prime visibility (Nakamura et al., 2012a) and arise even with a shorter prime duration (43 ms) (De Moor et al., 2007). Hence it is at least safe to assume that the observed effect of syllabic priming arises at either subliminal or preconscious stages preceding a generalized, top-down activation of the cerebral language network (Dehaene et al., 2006).

At the neural level, we found a robust effect of repetition enhancement in the left inferior lateral prefrontal area. This effect of repetition enhancement, unlike those observed in some previous studies (Muller et al., 2013; Reber et al., 2004), appeared even in earlier sessions of Experiment 1 and did not increase with the number of stimulus presentation. Additional analyses of response congruency further confirmed that repetition enhancement appeared with prime–target syllabic overlap, irrespective of the prime-induced response congruency which would interfere with later-stage decision processes. The left-predominant effect of repetition enhancement observed at the IFG (see Fig. 2C) is in good accord with the previously known dominance of the left hemisphere in lexical neighbor inhibition (Friedrich, 2005; Friedrich et al., 2013; Nakamura et al., 2012a; Perea et al., 2008). While the IFG is located far outside the ventral visual stream activated by masked visual words (Dehaene et al., 2005; Van Doren et al., 2010), the present finding seems to concur with the recent imaging study showing that weak or degraded visual stimuli may activate the left perisylvian language areas, including the superior temporal and inferior frontal areas (Axelrod et al., 2015).

Indeed, several ERP and magnetoencephalographic studies have shown that the same part of the left frontal area involved in speech production responds to written words much faster (~100 ms) than thought previously (Cornelissen et al., 2009; Klein et al., 2015; Pammer et al., 2004; Wheat et al., 2010). Such early activation has been proposed to rely on direct input signals from lateral occipital area bypassing the pOTS and reflect fast prelexical mapping from letter-strings onto articulatory codes (Wheat et al., 2010). In particular, this seems to concur with our finding that the neural priming at the left IFG was produced by the brief, preconscious exposure to masked words. It is also interesting to note that the observed part of the IFG (−46, 28, 20) is located identical to the left prefrontal region (−50, 17, 23) that is sensitive to unconsciously seen language stimuli (Axelrod et al., 2015). Together with these electrophysiological and fMRI data, the present results converge to suggest that the IFG constitutes a fast visual word processing

system that is anatomically distinct from the posterior occipito-temporal regions, including the classical visual word-form area associated with abstract orthographic codes and the LTC involved in lexico-semantic memory (Chertkow et al., 1997; Devlin et al., 2004; Nakamura et al., 2007; Tyler et al., 2003). Furthermore, this interpretation may provide neuroanatomical support for the notion that inhibitory effects of syllabic priming occur at the phonological, rather than orthographic, level of representations (Alvarez et al., 2004; Carreiras and Perea, 2002).

In Experiment 1, we also observed that stimulus–response congruency produced a distinct form of neural priming in the left PMd and LTC. This effect of congruency tended to increase in later sessions in parallel with behavioral priming effects at the PMd, but not at the LTC (see Fig. 3B). These findings are consistent with a previous fMRI study suggesting that response congruency priming during semantic judgment is mediated by two distinct neural systems, one in the LTC involved in lexico-semantic memory and the other in the dorsal premotor area involved in response preparation (Nakamura et al., 2007). Thus, the congruency effects seen in these regions each probably represent different stages of word processing from the one related to syllabic effects.

In Experiment 2, we used a more typical repetition priming paradigm to determine whether the effects of repetition enhancement observed in Experiment 1 reflected syllabic overlap or rather potential changes in visual attentional levels under the divided hemifield presentation procedure. We therefore manipulated the nature of prime–target relations such that primes and targets could overlap with each other at the whole-word level in “shared trials”, while keeping other experimental factors, such as task instructions and sequence of stimuli, almost identical to those in Experiment 1. As expected, behavioral results from Experiment 2 confirmed the classical pattern of facilitatory repetition priming, which is thought to reflect rapid activation of lexical representations during visual word recognition (Forster et al., 2003). Consistent with this finding, fMRI data also revealed the well-known effects of repetition suppression at the canonical coordinates of the “visual word-form area” (Dehaene et al., 2005). It is therefore likely that the rather atypical effects of repetition enhancement in Experiment 1 indeed reflect syllabic overlap itself, rather than other experimental factors.

Interestingly, moreover, ROI analyses revealed that the pOTS showed different patterns of priming between the two experiments, i.e., repetition enhancement in Experiment 1 and repetition suppression in Experiment 2, whereas the latter is known as a more typical form of priming during visual word recognition (Dehaene et al., 2001, 2010a; Nakamura et al., 2012b). Since the levels of attentional modulation and task difficulty should be identical between the two experiments (as described in RT analyses), these findings suggest that the directions of fMRI priming can change with the intrinsic nature of prime–target relations even when other experimental settings are equated. Importantly, this stimulus-driven change in repetition effects differs from the one observed by previous studies, where the directions of fMRI priming change with participants’ endogenous factors, such as attentional states and cognitive task contexts (Segaert et al., 2013). While the two experiments in the present study slightly differed in their precise settings (e.g., the number of trials/sessions), those minor differences seem to be insufficient to account for the observed difference in priming directions, which appeared even at the earliest stage of data acquisition (see Figs. 2C and 4C). Thus, our results suggest that even when observers’ attentional and cognitive states are kept constant, subtle changes in masked primes can reverse the directions of fMRI priming broadly in the left prefrontal and occipito-temporal regions.

On the other hand, it remains unclear how the directions of repetition effects changed with the nature of prime–target relations. Repetition suppression is generally thought to be the most common form of priming occurring in the occipito-temporal region during visual word recognition (Dehaene et al., 2005), but repetition enhancement is also known to occur in more anterior, fronto-temporal regions, including

the IFG (Kouider et al., 2007; Kuperberg et al., 2008; Raposo et al., 2006) and adjacent premotor area (Nakamura et al., 2007). While several different models have been proposed over the past decade to account for the cognitive and neural mechanisms of repetition effects, a recent review by Segaert et al. (2013) suggests that repetition enhancement is not a unitary phenomenon but can be caused by different cognitive factors, such as stimulus recognition, attention and memory retrieval. One such cognitive factor probably relevant to the present study is the notion that enhancement of neural activation occurs when some additional process operates on targets beyond task requirements (Henson and Rugg, 2003). That is, in Experiment 1, prime–target overlap is likely to activate lexical neighbors which need to be suppressed during visual identification of targets, whereas such additional inhibitory regulation would not occur when primes and targets have no shared segments. Indeed, repetition enhancement during reading might be mediated by those reverberant signals within the left-hemisphere language network, since the effect of enhancement is shown to appear either during conscious word recognition (Kouider et al., 2007; Kuperberg et al., 2008; Raposo et al., 2006) or during spoken production (Nakamura et al., 2007), both of which should produce strong top-down signals to the posterior task-relevant network (Dehaene et al., 2006). Similar to these conditions, recent electrophysiological studies, as mentioned above, suggest that the IFG rapidly activates to extract phonological codes from written word stimuli even prior to the activation of the pOTS and then generates top-down signals to the posterior temporoparietal regions (Klein et al., 2015; Woodhead et al., 2014). It is therefore plausible that the left IFG detects the prime–target relationship at the prelexical phonological level and then exerts top-down inhibitory influence over the posterior regions, including the pOTS, which may change the priming directions in these regions. Indeed, such top-down modulatory signals might play a role in the changes in the directions of fMRI priming (Eger et al., 2004; Nakamura et al., 2007).

In conclusion, we found that the behavioral inhibitory priming produced by lexical neighbors is associated with repetition enhancement in the left IFG. The present finding seems to strongly concur with the previous ERP data pointing to the left frontal region as a neural source of the similar inhibitory priming during reading (Friedrich et al., 2013) and suggests that the left inferior frontal region, a classical language area involved in speech production and distinct from the left occipito-temporal visual word-form system, constitutes a fast word-processing system sensitive even to masked words. Although the precise generation mechanism of fMRI priming is still open, the repetition effects observed here suggest that the directions of neural priming can be modulated not only by observers' endogenous factors but also by intrinsic properties of stimuli.

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