

Repetition priming without identification of the primes: Evidence for a component process view of priming

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The aim of the present study was to examine whether priming can occur due to recent perceptual processing of the same stimulus with minimal influence from conceptual process and also to investigate its underlying neural mechanisms using fMRI. Words were presented in mirror orientation in a word identification priming task. The presentation durations of the primes were titrated individually so that each participant could only identify approximately half of the primes, while the remainder disappeared before participants could identify the meaning of the word. A substantial behavioral priming effect was found when these unidentified primes were repeated later, suggesting that recent exposure to the perceptual processes without accessing the meaning is sufficient to prime later identical processes of the same repeated stimuli. Imaging data showed significant repetition suppression in several brain regions mediating perceptual, but not semantic or conceptual, processes. Together, our findings are consistent with the general predictions of transfer appropriate processing (TAP) and the component process view of priming, positing that priming is a function of more efficient cognitive processes that are repeated from study to test, and this increased efficiency is reflected in repetition suppression effects evident on fMRI. © 2007 Elsevier Inc. All rights reserved.

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Introduction

Priming refers to a change in speed, accuracy or bias in the processing of a stimulus, following prior experience with the same, or a related, stimulus. Previous studies have found that priming effects are usually greater when the physical form of the stimulus remains the same from the first to the second presentation (i.e. format-specific priming). This is true for studies manipulating sensory modality (e.g., visual vs. auditory; Clarke and Morton, 1983; Graf et al., 1985; Roediger and Blaxton, 1987; Schacter and Graf, 1989), symbolic form (pictures vs. words; Weldon and Roediger, 1987), script orientation (backwards or upside down vs.

normal; Kolers, 1975, 1979; Masson, 1986; Graf and Ryan, 1990) and sometimes type font or case (e.g., upper vs. lower case, hand-written vs. typed; Graf and Ryan, 1990; Marsolek et al., 1992, 1996; Gibson et al., 1993; Curran et al., 1996; Wiggs and Martin, 1998; but see Scarborough et al., 1977; Tardiff and Craik, 1989; Rajaram and Roediger, 1993 for failures to find type-specific priming).

Graf and Ryan (1990) proposed a transfer appropriate processing (TAP) framework (cf., Morris et al., 1977) to account for format-specific priming. TAP is based on the notion that remembering is best understood in terms of the cognitive operations that are engaged by different study and test activities (Kolers and Ostry, 1974; Kolers, 1975, 1979). Reading a word or sentence, for example, requires a particular set of sensory-perceptual and semantic-analyzing operations. Engaging these operations has the same effect as practicing a skill — it increases the fluency and efficiency with which the processes can be carried out subsequently. Performance on a priming test is thus facilitated depending on the extent of the cognitive operations that are used both on the study and test tasks. The greater the overlap in processes from study to test, the greater the facilitation. However, there is a major caveat to this general principle. Priming is also dependent upon how practiced these processes are — cognitive operations that are executed with a high degree of efficiency and skill will show little, if any, priming, whereas uncommon or unskilled operations will show greater facilitation after a single practice episode (Graf and Ryan, 1990; Ostergaard, 1998, 1999).

Recently, neuroimaging techniques such as functional magnetic resonance imaging (fMRI) have been used to identify brain regions mediating priming effects and their underlying neural mechanisms. A robust finding from these studies is that repeated stimuli (targets) usually exhibit reduced neural activations when comparing to their first presentations (primes) or other new stimuli (control items). This phenomenon has been referred to as the “repetition suppression effect” (for reviews, see Henson, 2003; Schacter and Buckner, 1998). The specific brain regions showing this effect depend on the priming task that is utilized and the format of the stimuli. For example, repetition suppression is usually found in posterior perceptual processing regions such as parietal and occipital regions during perceptual priming tasks (e.g., perceptual identification of degraded stimuli). In addition, when the priming task emphasizes

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conceptual analysis or semantic judgments about the stimuli, repetition suppression is often found in frontal regions such as left inferior frontal gyrus (LIFG). Consistent with a TAP framework, Henson (2003) proposed a “component process” theory of priming to account for the neuroimaging findings (see also Tenpenny and Shoben, 1992; Witherspoon and Moscovitch, 1989). This theory posits that several component processes are involved in completing a specific task. For example, making living/non-living judgments for pictures of objects requires visual analysis of the picture, identification of the object, retrieval of related semantic information, as well as processes involved in making the decision and executing the response. Each process is mediated by a neural network that will act more efficiently and require fewer neural resources if the same process has been engaged recently (indicated by repetition suppression). However, if a new process is involved only at the second encounter but not at the first encounter, the regions mediating this process can instead show increased neural activation when comparing second to first presentations (referred to as repetition enhancement). Thus, while behavioral priming may be manifest similarly across several different tasks as a decrease in reaction time or an increase in accuracy, fMRI and other neuroimaging methods may be useful in differentiating between the specific cognitive mechanisms underlying these various priming tasks.

Several fMRI priming studies have demonstrated regional specificity of repetition suppression based on the cognitive demands of the task. Wagner and his colleagues (2000) were particularly interested in identifying task-specific processes mediated by left prefrontal cortical regions. In their study, participants classified a series of words in either a perceptual decision task (upper or lower case) or a conceptual decision task (abstract or concrete). During subsequent scanning, participants classified the same set of words again, this time making conceptual judgments for all the words. Therefore, participants processed some words in the same conceptual decision task in both the study and test phases (within-task repetition), while other words were processed in the perceptual task during the study phase and the conceptual task during the test phase only (across-task repetition). Repetition suppression was observed in the anterior LIFG following within-task, but not across-task, repetition. In contrast, posterior LIFG showed repetition suppression in both the within-task and across-task repetition conditions. The findings are consistent with previous studies suggesting that anterior LIFG may mediate semantic analysis of format-invariant aspects of stimuli (Petersen et al., 1988; Domb et al., 1995), while posterior LIFG may involve the transformation of lexical information into phonological codes (Frost, 1998; for a review, see Poldrack et al., 1999). The within-task repetition condition engaged similar semantic and conceptual processes at study and test, resulting in repetition suppression in the anterior LIFG. Phonological processing of the stimuli, however, was likely engaged for all stimuli, regardless of the decision task, resulting in repetition suppression in the posterior LIFG for both priming conditions.

While Wagner et al. (2000) manipulated the overlap of the cognitive task demands across presentations while holding perceptual processes constant, Ryan and Schnyer (2007) varied the perceptual operations involved in a word identification task. They asked participants to identify a list of single words initially presented either in normal-image orientation (N) or in mirror-image orientation (M) and then repeated the words either in the same orientation (N–N and M–M) or in a different orientation (N–M and M–N). Presumably, perceptual processes in the N–M and M–N conditions

differed from study to test while the semantic content remained the same (activating the same semantic representations even though the physical form of the stimuli changed). On the other hand, in the N–N and M–M conditions, both perceptual and semantic processes were similar from study to test. The fMRI results showed evidence of format-specific priming, consistent with Henson’s (2003) component process view: greater repetition suppression was observed in regions for the M–M condition compared to the N–M condition that were specific to mirror-image reading, presumably mediating the rotation and transformation of letters necessary to identify these words. However, the N–M condition provided an additional finding. Unexpectedly, all regions that were involved in mirror-orientation reading showed significant repetition suppression at test, even though some of these regions showed no evidence of activation during study because the primes were presented in normal orientation.

This global repetition suppression effect observed in all mirror reading regions is inconsistent with a strict TAP view because TAP would predict that repetition suppression should occur only in regions that overlap from the initial N reading and the later M reading. Ryan and Schnyer (2007) suggested that this result might reflect the influence of top–down modulation. This view is also consistent with Dale and his colleagues (2000) who demonstrated that when words were repeated in a size judgment task, priming effects were widespread across the entire cortical network involved in word processing. In addition, they reported that electrocortical repetition effects did not begin until well after the initial perceptual analysis of a stimulus was complete (200–260 ms post-stimulus onset). Ryan and Schnyer (2007) suggest that there may be two distinct and perhaps interactive bases for priming. Priming may be mediated either by “top–down” or “bottom–up” processing of words, depending upon the specific circumstances of the test. A recent presentation of a word in any form that fully engages the semantic representation of that word may prime all aspects of a repeated presentation, semantic and perceptual. Increasing the efficiency of semantic processing will serve to disambiguate the perceptual processing of a repeated item presented in a new format, and this effect will be particularly evident when the task is unfamiliar or difficult, as in the case of reading words in an unfamiliar orientation or in a degraded form. Accordingly, top–down modulation may produce repetition suppression even in perceptual regions that are not engaged in the initial processing. A strong version of this view may claim that all priming effects are produced by top–down modulation, which would explain why repetition effects in MEG or EEG studies (Dale et al., 2000) did not occur much earlier during perceptual analysis. Surprisingly, few studies, to our knowledge, have examined this issue directly. Most neuroimaging (and behavioral) studies on priming have used tasks that require participants to fully identify the meaning of the stimuli. Therefore, it is difficult to conclude from these studies whether priming can occur at early perceptual processing stages without top–down modulation.

One line of studies addressing this issue used a masked priming paradigm, where the primes are presented very briefly (e.g., 30 ms) and followed and/or preceded by masks, so that participants are not consciously aware of the existence of the primes, hence relatively little conceptual processing of the primes or top–down modulation should occur. This is presumably a good paradigm to study priming without top–down modulation, however it is in fact still controversial regarding how “deeply” the primes are processed in the masked priming paradigm. For example, some studies have found significant semantic priming effects using masked priming para-

digms (e.g., Bodner and Masson, 2003), indicating that even when the primes are not consciously identified, there may still be conceptual processing occurring. This is especially true when the task is relatively easy and automatic (e.g., reading a word in normal orientation), therefore the conceptual processing may be accomplished without conscious awareness. In addition, masked primes are usually presented very quickly (at most about 60 ms) and their effects only last for few seconds at most. The magnitude of masked priming effect is also usually very small (about the same time scale as the prime duration). Several researchers have suggested that masked priming may involve mechanisms that are different from long-term priming (e.g., activation vs. weight-based memory, O'Reilly and Munakata, 2000; lexical vs. episodic processing, Forster and Davis, 1984), and thus the results may not apply directly to long-term priming, which is the focus of the present study.

To address the top-down modulation issue, we designed the current study in order (a) to determine whether long-term priming can occur due to recent perceptual processing of the same stimulus with minimal influence from top-down conceptual modulation and (b) to examine the degree to which regional patterns of repetition suppression will be influenced by incomplete processing of the prime. We achieved this goal by presenting words in a modified mirror word identification paradigm (Ryan and Schnyer, 2007; Poldrack et al., 1998; Poldrack and Gabrieli, 2001) in which words were processed perceptually for a certain amount of time (up to few seconds) but disappeared at about the time participants could identify the meaning of the word. The presentation durations of the primes were titrated individually so that each participant could only identify approximately half of the primes. When the identified and unidentified primes were later repeated, participants were now given sufficient time to identify all the items.

According to a TAP view of priming, unidentified primes should produce behavioral priming because some of the same operations (presumably mainly perceptual) will be repeated from unidentified primes to their targets, even though identification is not completed at first presentation. Furthermore, the component process view of priming would predict that only regions mediating perceptual processes will exhibit repetition suppression, while regions related to accessing meanings or the semantic/conceptual processes followed automatically by the identification of words will not. Alternatively, according to a strong top-down modulation view, priming will only occur in the identified prime condition, and repetition suppression will not be observed within the unidentified prime condition, even in areas presumed to mediate perceptual analysis.

Methods

Participants

Participants (10 females, 7 males) were all right-handed native English speakers, ages 18 to 30 years (mean age 20.9) with 12 to 21 years of education (mean 14.0). They were screened to exclude drug and/or alcohol abuse, neurologic disorder, significant head injury, psychiatric illness and contraindications to MRI. All procedures were approved by the Human Subjects Committee at the University of Arizona.

Materials

Eight hundred words were randomly selected for use in the experiment, 5 to 8 letters in length, with medium to high word

frequency (20 to 300 occurrences per million; Kucera and Francis, 1967). Mirror-image reading has been shown to engage a letter-by-letter reading strategy (Graf and Ryan, 1990; Poldrack et al., 1998) so that even when a word is not fully processed, a few letters at the beginning of a word will have already been identified. To prevent partial priming from processing the same first few letters of the prime, no words shared the same first four letters. For example, the word “action” was selected, but “acting”, “active” and “activity” were not. In addition, no words shared the same meaningful stem. For example, “anybody” was selected, but “anyhow” and “anyone” were not.

The 800 words were quasi-randomly assigned to eight lists, each containing 100 words, ensuring that each list was similar in distribution of word lengths and word frequencies. A pilot study with 10 participants showed that the mean and median reading times in mirror-image orientation of the eight word lists did not differ from one another.

Words were presented centered on a computer screen (or video goggles in the scanner) in lower case, in bright green 80-point font on a black background, using Arial Bold font. A Windows-based program DMDX (Forster and Forster, 2003) was used to present all stimuli and to record responses, response times (RTs) and stimulus onset times in the experiment, both inside and outside the scanner.

Procedure

Each participant underwent a practice session and a pretest session outside the scanner. One of the eight 100-word lists was used for the practice session, and a second list was used for the pretest. These two lists were the same for all participants. They then performed three test blocks while undergoing fMRI scanning, each containing two lists. The six test lists were counterbalanced for order and conditions across participants.

Participants were told that the aim of the study was to investigate reading processes. They were instructed that they would see symbols or words presented in mirror-image orientation on the computer screen. They were instructed to identify the word and then click the left mouse button with their right index finger as quickly as possible. When a symbol string (“!+!+!+!”) was presented, they had to click the right mouse button with their right middle finger as quickly as possible. The trials with symbol strings were used as a visual-motor control (VM condition) for fMRI analysis.

The presentation sequence in each trial (including practice, pretest and test trials) was similar (see Fig. 1). Each trial contained a 500 ms crosshair (+) followed by a word or a symbol string (“!+!+!+!”) and then a 630 ms backward mask (#####). Trials were separated by a 350 ms blank screen. During the practice session, 100 mirror-image words and 15 VM trials were presented. In the first half of the practice session, the presentation of words and symbols was self-paced, with stimuli remaining on the screen until a response was made. In the second half, the stimuli remained on the screen for various display durations ranging from 700 ms to 5 s. This portion of the practice session was designed to better represent the stimulus durations that would be presented later on in the test blocks, where display durations for primes would be much shorter (described in detail below). Participants were encouraged to respond as quickly as possible to each word because otherwise the item might disappear from the screen. However, it was emphasized that accuracy was very important. They should make sure they indeed identify the word before responding. On the other hand, to ensure that participants

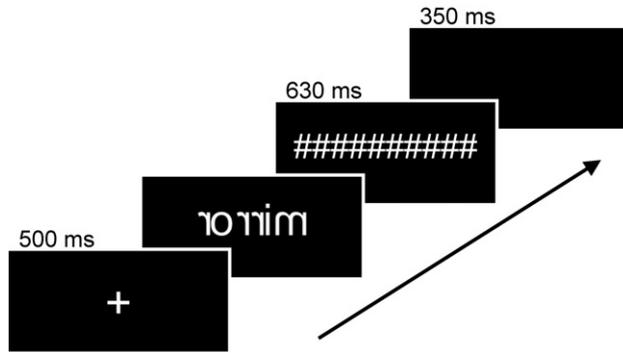


Fig. 1. An example of the presentation sequence of a trial. The display duration of the stimulus item (in the second frame) depended on its own trial type. Targets, control and VM items were presented for up to 4 s (self-paced). Primes instead were not self-paced and were displayed with a fixed duration in the same test block (see text for detail).

always had a chance to respond if they did identify a word, they were instructed that even after an item disappeared, they could still make a response before the backward mask disappeared. During the test blocks, responses were measured until the end of the mask displays for each trial. Participants were told that some words would be more difficult to identify than others within the allotted time, and that after the backward mask disappeared, they should just move on and prepare for the next trial. They were also informed that sometimes the words may be repeated because we needed many trials in our experiment, but their primary task was simply to read each word as quickly as possible without sacrificing accuracy.

After the practice session, a pretest was used to measure each participant's mirror reading speed in order to optimize the display durations for their primes so that the time of the primes on the screen would be just enough for them to identify approximately half of them. The pretest contained 100 mirror words and 25 VM control items that were all displayed on the screen for up to 5 s so that participants had sufficient time to respond to each item. An additional 50 filler mirror words were randomly included in the list, too, with display durations ranging from 700 to 2500 ms in order to make the pretest more similar to the test blocks that would be presented later in the scanner. The 25 VM control items and 50 filler words were not used to determine the final display duration.

After pretest, the median RT of the 100 pretest mirror words was calculated for each participant. This value, multiplied by 0.5, was then used as the display duration for the primes in the first test block. Pilot studies showed that this value was optimal for ensuring 50% identification rate in the first test block.

Participants then moved into the scanner to perform the three test blocks while undergoing fMRI. Stimuli were presented via high-resolution VisuaStim digital goggles (Resonance Technology Inc., Los Angeles, CA) and response times were collected using an MRI compatible computer mouse placed in the participant's right hand. Each test block contained 100 primes (one of the six test lists), 100 targets (the same test list repeated), 100 control items (a second test list, presented only once, which served as the unprimed baseline condition for calculating priming) and 50 VM trials. Trial types were mixed in a pseudo-random order within each test block, with a lag of 8 to 17 intervening trials between primes and their targets (average lag 12.82). A total of 300 primes, 300 targets, 300 control words and 150 VM items were presented across three test blocks for each participant.

In the first test block, target words, control words and VM trials were presented for up to 4 s which was sufficient for participants to identify most of the words. For these trials, presentation was self-paced so that items would disappear from the screen whenever a response was made or when 4 s had passed. Primes, as described earlier, were presented for a fixed display duration calculated from the pretest for each participant. These trials were not self-paced so that a response to the prime would not advance the presentation to the next item immediately. Therefore, the identified and unidentified-primers were present on the screen for the same amount of time.

In the second and third blocks, the display durations for targets, control words and VM items were the same (up to 4 s). However, to ensure that only approximately half of the primes were identified across three test blocks, the display durations for primes were calibrated after each test block based on the rules listed in Table 1. These rules were derived from pilot studies. If the percentage of identified and unidentified primes in the previous test block differed from 50%, the display duration of primes in the following test block was shortened or lengthened in order to achieve 50% of total identification rate for primes.

Image acquisition

Images were acquired on a GE 3T whole-body echo-speed MRI system. A set of 3-plane localizer images were collected first in order to align a set of T1-weighted images (matrix=256×256, TR=625 ms, TE=13 ms, FOV=24 cm, number of sections=27, 4 mm, interleaved, no skip) parallel to the anterior-posterior commissural plane covering approximately the whole brain. Following acquisition of the T1 anatomical images, functional images were acquired in three scans. Each scan corresponded to a behavioral test block. Functional images were acquired in the same anterior-posterior commissural plane using a single-shot spiral in-and-out acquisition protocol (Glover and Lee, 1995; Glover and Law, 2001; matrix=64×64, TR=2000 ms, TE=40 ms, FOV=24 cm, flip angle=90, number of sections=27, 4 mm, no skip). The first functional scan

Table 1

Calibration rules to decide display duration of the primes for the second and third test blocks

(# of identified primes) – (# of unidentified primes)	Calibration coefficient
<–80	1.6
–80 to –51	1.5
–50 to –31	1.4
–30 to –21	1.2
–20 to –10	1.1
–9 to –1	1.0
0 to 10	0.9
11 to 20	0.8
21 to 30	0.7
31 to 50	0.5
51 to 80	0.3
>80	0.1

When the difference of accumulated numbers of identified versus unidentified primes (across the previous test blocks) fell into the specified range, the prime display duration in the following test block was calibrated by taking the prime display duration in the last block multiplied by the corresponding calibration coefficient in the right column of this table (see text for more detail).

was collected with a total of 456 repetitions taking 15 min, 12 s to complete. For subsequent scans, the number of repetitions was adjusted depending on the reading speed of the particular participant (ranging from 365 to 590 repetitions). After completion of the functional scans, a high resolution SPGR volume was also acquired (1.5 mm sections covering whole brain, matrix=256×256, flip angle=30, TR=22 ms, TE=8 ms, FOV=25 cm) but not used for analysis in the present study.

Behavioral analysis

Trials were sorted into eight trial types based on each participant's own responses (see Table 2). First, trials with incorrect responses (wrong mouse button was pressed), as well as trials with no responses (except for primes), and trials with RTs less than 300 ms for mirror word trials and less than 200 ms for VM trials were excluded from further analysis (specified as "error trials"). Pilot data indicated that items with very short RTs were outside the distribution of normal responses and only occurred as errors. In addition, outliers with RTs longer than 3 standard deviations from the mean of the combined valid control and target trials were also excluded (less than 1% of the total trials). If a prime or target was marked as an error trial, its corresponding target or prime trial was excluded as well. Valid VM trials were sorted as VM trials.

The remainder of the valid trials were sorted into either identified-prime (IP-primes, IP-targets and IP-controls) or unidentified-prime conditions (UP-primes, UP-targets and UP-controls). Primes were split into identified primes (IP-primes) and unidentified primes (UP-primes) depending upon whether or not a valid response was recorded. Targets were also sorted into two trial types based on their corresponding primes: targets whose corresponding primes were identified (IP-targets) and targets whose corresponding primes were unidentified (UP-targets). However, note that these UP-targets themselves were identified; only the primes for these target words were unidentified.

Behavioral priming effects are normally calculated by comparing the RTs for unprimed items versus primed items (targets). Unprimed items can either be the primes themselves or an additional set of similar but unrepeated items that provide a baseline for performance. In our design, because by definition there were no RTs recorded for UP-primes, we could not calculate the priming effect in the unidentified-prime condition by comparing the RTs for UP-targets and UP-primes directly. Therefore we compared UP-targets with an appropriate set of unprimed control words (UP-controls). In the present study, IP-primes and UP-primes were differentiated based on

reading difficulty, such that IP-primes were easier to identify for a given individual than UP-primes within the same display duration. Since the word lists used as baseline control and prime/target trials had similar properties and were counterbalanced across conditions, the RT distributions should be similar across all lists. Therefore, control trials were also split into IP-control and UP-control trials (Table 2) based on the distribution of IP-primes and UP-primes in each test block for each participant. If a response for a control trial was shorter than the display duration of the primes in that test block, it was categorized as an IP-control trial. The number of IP-controls and the number of IP-primes with RTs shorter than the display duration of the primes should be similar and have similar distributions because they were drawn from word lists with similar distributions and separated with the same cutoff. Furthermore, because we allowed participants to respond to primes until the end of the mask, some responses to the primes occurred during the period while the mask was still on the screen. To match these primes with control items, we paired each prime from the mask period with the control trial that had the closest RT in that test block so that the number of items and distribution of RTs for IP-controls and IP-primes in the mask period would be similar. The remainder of the control trials were categorized as UP-controls, which would be compatible with UP-primes.

After the trials were sorted, median RTs were calculated for each trial type for each participant (collapsed across three test blocks). Behavioral repetition priming effects were then calculated using the means of median RTs. In the identified-prime condition, priming was calculated by comparing IP-targets with IP-control words or by comparing IP-targets with IP-primes. Priming calculated in these two ways was expected to produce similar results. In the unidentified-prime condition, priming was calculated by comparing UP-targets with UP-control words.

Image analysis

Images were reconstructed offline and then analyzed in SPM2 (<http://www.fil.ion.ucl.ac.uk/spm>). All volumes were realigned to the first volume to correct for movement. The data in each section were interpolated in time to match the acquisition time of the middle section. Spatial normalization parameters were estimated by warping each participant's mean functional image to the standard MNI (Montreal Neurological Institute) EPI template (Ashburner and Friston, 1999). Normalized images were resliced to 3×3×3 mm voxels and smoothed with an isotropic 8 mm FWHM Gaussian kernel. The timeseries in each voxel was highpass-filtered to 1/128 Hz and scaled to a grand mean of 100, averaged over all voxels and scans within a session.

Statistical analysis was performed in two stages (Penny, 2004). In the first stage, neural activity was modeled by a delta function at stimulus onset. The ensuing BOLD response was modeled by convolving these delta functions with a canonical hemodynamic response function (HRF) and its temporal and dispersion derivatives (Friston et al., 1998). The resulting timecourses were downsampled at the midpoint of each scan (corresponding to the middle section) to form covariates in a General Linear Model. Covariates were modeled for the canonical HRFs of the eight trial types (described earlier), their time and dispersion derivatives and a single covariate representing the mean (constant) over scans (only canonical HRF covariates were used to make contrasts and move to second level analyses). Temporal autocorrelation of the errors was accommodated by an AR(1) model, the parameters of which represent

Table 2
Trial types for behavioral and fMRI analysis

Trial types	Description
(1) IP-primes	Identified primes: primes with valid response recorded
(2) UP-primes	Unidentified primes: primes with no responses recorded
(3) IP-targets	Targets whose primes were identified
(4) UP-targets	Targets whose primes were not identified
(5) IP-controls	Control items for identified primes
(6) UP-controls	Control items for unidentified primes
(7) VM trials	Visual-motor control items as a baseline for fMRI contrasts: symbol strings ("!+!+!+!")
(8) Error trials	Incorrect responses, no responses (except for primes), outliers, and trials with too short RTs (less than 300 ms for mirror word trials and less than 200 ms for VM trials)

hyperparameters governing the nonsphericity of the error covariance and which were estimated together with the parameters for each covariate using Restricted Maximum Likelihood (Friston et al., 2002).

Contrasts of parameter estimates comprised the data for the second-stage analyses, which treated participants as a random effect. SPMs were thresholded for 5 or more contiguous voxels surviving $p < 0.001$ threshold (uncorrected for multiple comparisons) unless otherwise specified. Stereotactic coordinates were generated in the standard MNI brain by SPM originally. The SPM Anatomy Toolbox (http://www.fz-juelich.de/inb/inb-3//spm_anatomy_toolbox; Eickhoff et al., 2005, 2006) was used to transform these coordinates into the Talairach and Tournoux (1988) space and to estimate neuroanatomical regions and the Brodmann's areas. All the coordinates reported or cited here are in Talairach and Tournoux space.

Results

Behavioral results

The mean number of valid trials (collapsed across three test blocks) obtained in each trial type is listed in Table 3. The means ranged from 124.29 to 142.65 (mean = 133.89) which provided reasonable numbers of trials for later behavioral and fMRI analyses. The numbers of the three trial types in either the identified-prime or the unidentified-prime condition were not significantly different from each other, $F^2 < 2$, ns.

The means and standard deviations of median RTs for each trial type are also listed in Table 3. As expected, RTs for IP-controls (mean 824.60 ms) were not significantly different from IP-primers (821.99 ms), $t(16) < 1$, suggesting that IP-controls provided a reasonable estimate of RTs for IP-primers, and the remainder of the items (UP-controls) should therefore be a reasonable estimate of RTs for UP-primers.

A repeated-measures ANOVA was conducted to test two factors, "identification" (identified, unidentified) and "repetition" (controls, targets). As expected, a significant main effect for identification, $F(1,16) = 23.52$, $p < 0.001$, indicated that items in the unidentified-prime conditions (UP-controls and UP-targets) showed longer RTs than items in the identified-prime conditions (IP-controls and IP-targets). A significant main effect for repetition was also found, $F(1,16) = 20.69$, $p < 0.001$, indicating a general priming effect such

that RTs for repeated items (IP-targets and UP-targets) were shorter than RTs for non-repeated items (IP-controls and UP-controls). Importantly, a significant interaction was also found ($F(1,16) = 22.73$, $p < 0.001$), indicating that the magnitude of priming effects differed in the identified-prime and unidentified-prime conditions. In the unidentified-prime condition, a substantial priming effect (446.22 ms) was observed when comparing UP-controls and UP-targets (paired $t(16) = 4.77$, $p < 0.0001$). However, in the identified-prime condition, the RT difference between IP-targets and either IP-primers or IP-controls did not approach significance, paired t 's(16) = 1.29 and 1.38, ns, respectively.

One possible reason that behavioral priming was not observed in the identified-prime condition is that IP-primers in our study were self-selected based on the ability of the participant to identify them within a brief display duration and were thus the easiest items to identify for a given individual. It has been demonstrated previously that the magnitude of behavioral priming effects increases with increasing difficulty, complexity and unfamiliarity of the task (Graf and Ryan, 1990; Ryan and Schnyer, 2007). For example, Ostergaard (1998, 1999) has shown that degraded words that are the easiest to identify within a larger group of words (indicated by identification speed) show little or no priming. If this were the case, then we would predict that within the identified-prime condition, trials with longer RTs might show significant priming effects while trials with shorter RTs might show little or no priming.

To test this hypothesis, we split IP-primers into four quartiles based on the distribution of their RTs and then compared the RTs for IP-primers and their corresponding IP-targets within each quartile. The results indicated that RTs for primes and targets diverge as they become longer. The 4 (Speed: RT groups of the primes) \times 2 (Repetition: IP-primers or IP-targets) repeated-measures ANOVA showed a significant main effect for speed, $F(1,16) = 22.56$, $p < 0.001$, but not for repetition, $F(1,16) < 3$, ns. However, the interaction between speed and repetition was also significant, $F(1,16) = 20.23$, $p < 0.001$. Paired t -tests showed no significant priming effects for the middle two RT groups (t 's(16) < 1.5 , ns), but significant priming for the longest RT group, $t(16) = 4.07$, $p < 0.002$, with target RTs on average 252 ms faster than prime RTs. Interestingly, in the fastest RT group, the difference between primes and targets was significant, but in the opposite direction, with longer average RTs for targets than primes, $t(16) = 3.37$, $p < 0.005$. When calculating the correlation between initial reading speed (mean IP-prime RT for each individual at each of the four quartiles) and priming (the facilitation effect for subsequent reading of the same items), a linear relationship with a Pearson's r coefficient of 0.65 ($p < 0.001$, two-tailed) was found. Taken together, these results indicated that even though the overall priming effect was not significant in the identified-prime condition, the longer RT trials in this condition showed significant priming.

Imaging results

Regions involved in mirror reading

Regions showing significant activation ($p < 0.001$, uncorrected) during new mirror reading (IP-controls and UP-controls) compared to the VM control condition are listed in Table 4. The results were consistent with previous studies using a similar paradigm (Ryan and Schnyer, 2007; Poldrack and Gabrieli, 2001; Poldrack et al., 1998) showing that mirror reading was associated with activation along both the dorsal and ventral visual streams, including bilateral occipital, temporal and parietal regions. Frontal regions also showed

Table 3

Mean response times (RTs), mean numbers of valid trials and their standard deviations (SD) in different conditions across participants

Condition	Trial types	Mean RTs (ms)	SD	Mean trials	SD
Identified-prime	IP-primers	821.99	365.70	124.29	24.12
	IP-controls	824.60	368.90	126.47	22.00
	IP-targets	792.66	320.19	124.29	24.12
Unidentified-prime	UP-primers	(1161.41)	(650.88)	142.65	36.35
	UP-controls	1444.80	848.58	138.24	45.11
	UP-targets	998.58	497.36	142.53	36.35
Baseline	VM	557.79	67.22	138.76	13.72

Trial types are described in Table 2.

Note: UP-primers were primes for which participants did not make a response, therefore no RTs were recorded for these trials. Presented is the mean recording time cutoff (close to the display durations of their UP-primers).

Table 4
 Activations for mirror reading: new mirror words (IP-controls & UP-controls) vs. visual-motor control

Brain region	BA	Cluster size (voxels)	x	y	z	Z-score	
<i>Mirror reading > VM</i>							
Occipital/temporal lobes							
L	Cuneus	19	6	-27	-94	41	3.99
R	Cuneus	19	42	42	-91	20	4.81
L	Occipital/fusiform/inf. temporal	17/18/19	419	-42	-85	-10	7.68
R	Occipital/fusiform/inf. temporal	17/18/19	180	39	-82	-1	5.93
L	mid./sup. temporal	21/22	161	-51	-39	3	7.18
R	Mid./sup. temporal	21/22	28	57	-16	-4	5.17
L	Inf. temporal	20	9	-39	-22	-19	5.40
Parietal lobes							
L	Precuneus/sup. parietal	7/19	144	-18	-67	53	6.32
R	Precuneus/sup. parietal	7/19	55	27	-76	38	4.98
L	Post. cingulate	-	12	-15	-58	17	4.97
R	Post. cingulate	-	5	18	-55	14	4.37
L	Supramarginal	40	5	-39	-43	35	4.31
Frontal lobes							
L	Ant. and post. IFG to precentral gyrus/SMA/mid. cingulate/	44/45/6/4	1200	-42	-1	62	6.57
R	Ant. and post. IFG to precentral gyrus/SMA/mid. cingulate/basal ganglia	44/6/4	1394	42	11	20	6.23
R	Ant. IFG	47	12	42	29	-10	4.49
L	Sup. med. frontal	8	45	-9	41	47	4.97
L	Sup. med. frontal	10	10	-9	59	29	4.80
Other regions							
L	Ant. hippocampus/amygdala	-	85	-18	-16	-13	6.37
R	Ant. hippocampus/amygdala/ parahippocampal	-	51	21	-16	-19	4.79
R	Hippocampus	-	12	24	-34	5	4.46
L	Basal ganglia	-	29	-21	2	14	4.10
<i>VM > mirror reading</i>							
R	Lingual/fusiform	18/19	132	24	-66	-43	6.29
B	Precuneus	7	30	0	-70	50	5.56

Only clusters with an extent of at least 5 voxels were listed. For all Z-scores, p 's < 0.001, uncorrected. BA = Brodmann's area; x, y and z coordinates in Talairach space; L = left; R = right; B = bilateral; mid. = middle; sup. = superior; inf. = inferior; med. = medial; ant. = anterior; post. = posterior; IFG = inferior frontal gyrus; SMA = supplementary motor area.

extensive activations along inferior (both anterior and posterior parts), middle and superior frontal and precentral gyri bilaterally, as well as several medial superior frontal and anterior cingulate regions (see also Fig. 2A). In addition, activations were also found in bilateral anterior medial temporal lobe (MTL) regions, right posterior hippocampus and bilateral basal ganglia.

Repetition effects in the identified-prime condition

Despite the finding of priming for only a subset of the primes and targets in the identified-prime condition with longer RTs, IP-targets overall showed significantly reduced activation comparing to IP-primes (repetition suppression) in bilateral middle temporal gyri, bilateral anterior inferior frontal gyri (IFG), right middle frontal gyrus, left insula and the midbrain/pons region ($p < 0.001$, uncorrected; see Table 5 and Fig. 2B). Note that the repetition suppression effects in this condition were generally more prominent in the right hemisphere than their homologous regions in the left hemisphere, including the inferior frontal regions and the middle temporal regions. In addition, activation reductions in bilateral IFG were mainly anterior (BA 44/45/47). This pattern of repetition suppression is consistent with previous studies using a

similar priming paradigm and contrasts (Ryan and Schnyer, 2007; Poldrack and Gabrieli, 2001; Poldrack et al., 1998). The opposite contrast (IP-targets > IP-primes) did not show significant repetition enhancement effects at $p < 0.001$, uncorrected, in any brain region.

Repetition effects in the unidentified-prime condition, comparing targets to controls

When compared to UP-controls, UP-targets showed significant signal reductions in multiple brain regions involved in mirror reading ($p < 0.001$, uncorrected, see Table 6 and Fig. 2C). These regions included bilateral occipital lobe, inferior temporal and fusiform gyri, right middle temporal gyrus, precuneus, bilateral MTL (bilateral anterior hippocampus and left posterior hippocampus), basal ganglia/thalamus and bilateral frontal regions. The frontal regions included bilateral precentral and middle frontal gyri (BA 6) and right anterior inferior frontal gyrus. Importantly, only the right hemisphere showed repetition suppression in a small portion of the anterior IFG (BA 45). The left hemisphere only showed repetition suppression in a posterior precentral region (BA 6). This finding is in contrast to the activation reductions for identified

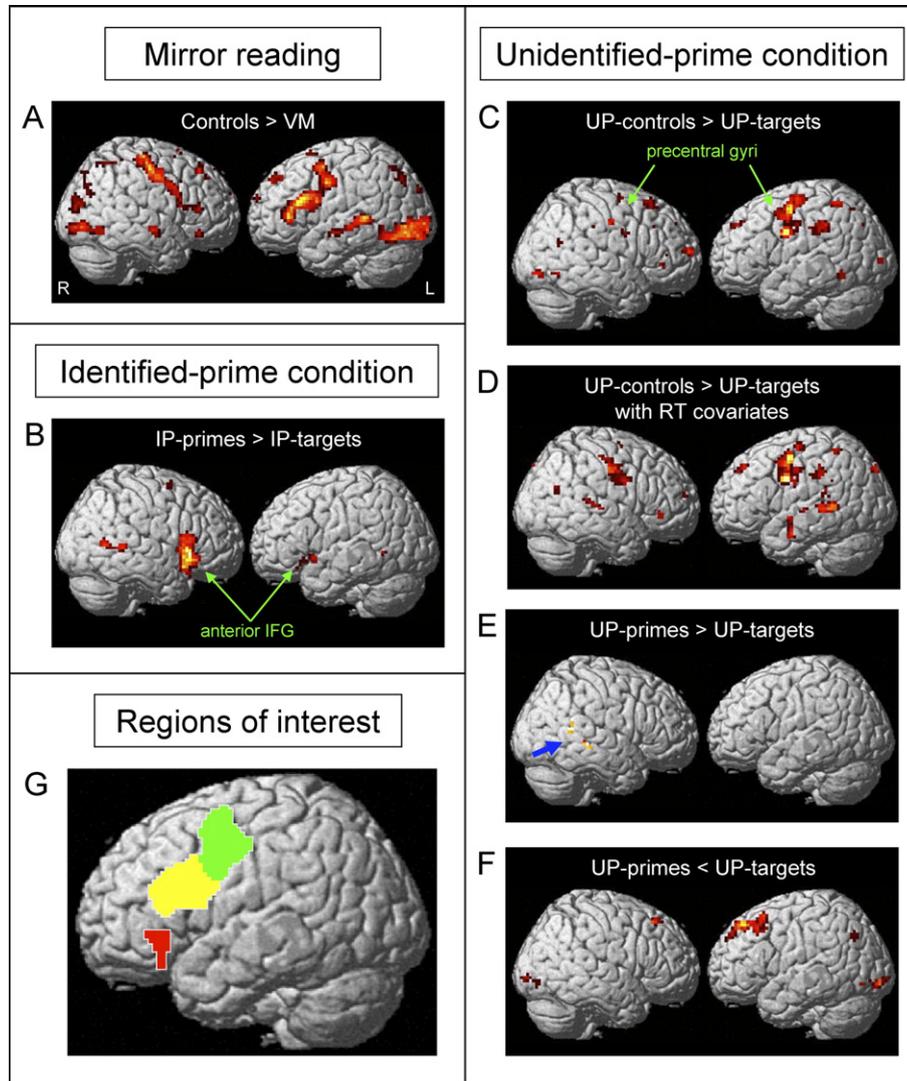


Fig. 2. fMRI results of mirror reading and repetition effects. Activations were all thresholded at $p < 0.001$, uncorrected. (A) Brain regions related to reading new mirror words (IP-controls & UP-controls > VM showing in red and IP-controls & UP-controls < VM showing in blue). (B) Brain regions exhibiting repetition suppression when comparing identified primes to their targets (IP-primers > IP-targets), including bilateral anterior inferior frontal gyri, middle temporal gyri, right middle frontal gyrus, left insula and the midbrain/pons region. (C) Brain regions exhibiting repetition suppression when comparing controls to targets with unidentified primes (UP-controls > UP-targets), including several regions involved in mirror reading. Note that, in the left frontal cortex, only the precentral, but not the anterior IFG, region showed repetition suppression. (D) Brain regions exhibiting repetition suppression when comparing controls to targets with unidentified primes (UP-controls > UP-targets), controlled for RT. A similar pattern was found as the previous contrast. (E) Brain regions exhibiting repetition suppression when comparing unidentified primes to their targets (UP-primers > UP-targets). Only few voxels in the right superior/middle temporal region (identified by the blue arrow) showed repetition suppression. (F) Brain regions exhibiting repetition enhancement when comparing unidentified primes to their targets (UP-primers < UP-targets). (G) Three ROIs. Red: BA 45/47; yellow: BA 44; green: BA 6.

primers that were observed in a more extensive region of bilateral anterior IFG (BA 44/45/47).

Consistent with the identified-prime condition, UP-targets did not show significant repetition enhancement effect when compared to UP-controls.

Because the behavioral priming effect found in the unidentified-prime condition was quite substantial (446 ms) and our presentations to the target and control trials were self-paced, it is possible that the differences in signal amplitude were simply reflecting the differences in the time each word remained on the screen. To rule out this confound, we conducted a separate imaging analysis using a similar SPM design matrix (without temporal and dispersion derivatives) but adding in RT as a covariate (parametric modulation)

for each trial type (IP-primers, IP-controls, IP-targets, UP-controls and UP-targets, but not UP-primers because these trials did not have RTs recorded). The results of the contrast comparing UP-controls to UP-targets were essentially identical to the original analysis without RT covariates, showing repetition suppression effects in all the same regions including frontal cortex, parietal cortex, medial temporal regions and right inferior temporal and fusiform gyri (see Fig. 2D), with some additional voxels extending more anteriorly in bilateral superior and middle temporal gyri. The only difference at $p < 0.001$, uncorrected, was that no repetition suppression effects were found in the occipital cortex and left inferior temporal/fusiform gyrus with the addition of RT covariates. However, with a more liberal threshold ($p < 0.005$, uncorrected) these regions showed repetition suppression

Table 5
Brain regions exhibiting priming related activation changes following identified primes, comparing targets to primes

Brain region		BA	Cluster size (voxels)	x	y	z	Z-score
<i>Repetition suppression: IP-primes > IP-targets</i>							
L	Mid. temporal	37	5	-54	-58	5	4.49
R	Mid. temporal	21	58	57	-64	14	5.81
L	Ant. IFG	45/47	28	-33	17	-4	4.66
R	Ant. IFG	44/45	266	42	20	-4	8.11
R	Mid. frontal	6	5	39	-1	68	4.47
L	Insula	-	14	-45	8	-4	4.72
L	Midbrain/pons	-	11	-6	-37	-22	4.64
<i>Repetition enhancement: IP-targets > IP-primes</i>							
N/A							

Only clusters with an extent of at least 5 voxels were listed. For all Z-scores, p 's < 0.001, uncorrected. BA = Brodmann's area; x, y and z coordinates in Talairach space; L = left; R = right; mid. = middle; ant. = anterior; IFG = inferior frontal gyrus.

effects as well. This finding suggests that the visual cortex and left inferior temporal/fusiform gyrus might be more sensitive to the duration of the visual presentation of the stimuli. However, overall, the covariate analysis shows that even when controlling the display durations of the stimuli on the screen, the pattern of repetition suppression was similar across brain regions.

Direct comparison of UP-targets and UP-primes

While UP-targets showed robust and widespread repetition suppression compared to UP-controls, a very different pattern of activation was evident when contrasting UP-targets with UP-primes, where identification of the prime did not occur (see Table 7). Compared to UP-primes, UP-targets showed significant increased activation ($p < 0.001$, uncorrected), or repetition enhancement, in a widespread network of brain regions, including bilateral inferior occipital cortex, posterior parietal regions, middle/superior frontal gyri, MTL regions and the right cerebellum (see Fig. 2F). In the opposite contrast comparing primes > targets, only few voxels in the right middle and superior temporal gyri exhibited significant repetition suppression effects at $p < 0.001$, uncorrected (see Fig. 2E).

Region of interest (ROI) analysis comparing identified-prime and unidentified-prime conditions in left frontal cortex

An ROI analysis was used to further elucidate the differential repetition suppression effects found in the left frontal cortex for the identified-prime and unidentified-prime conditions. Three frontal regions (BA 45/47, BA 44 and BA 6), described in detail in Gold et al. (2005) were selected based on previous studies examining semantic and phonological processing in frontal regions (Ryan and Schnyer, 2007; Petersen et al., 1989; Raichle et al., 1994; Buckner et al., 1995; Poldrack et al., 1999; Wagner et al., 2000; Gold and Buckner, 2002; Jonides et al., 1998; Paulesu et al., 1993). The center coordinates of the three ROIs (BA 45/47: -39, 25, -16; BA 44: -48, 16, 21; BA 6: -50, -7, 36) were determined by the closest local maxima coordinates obtained from our analysis identifying regions involved in mirror word reading (described earlier) to the coordinates used in Gold et al. (2005; BA 45/47: -45, 35, -4; BA 44: -47, 17, 24; BA 6: -55, -1, 28). The ROIs were defined by all the significant voxels in the mirror word reading contrast ($p < 0.01$, uncorrected) within a 20 mm radius of these three coordinates, providing three non-overlapping regions (see Fig. 2G). Data for the contrasts of comparing each trial type (IP-primes, IP-targets, UP-

controls and UP-targets) to the VM control condition were extracted by the MARSBAR toolbox (ver. 0.38; Brett et al., 2002; <http://marsbar.sourceforge.net>) for each participant and the means were calculated for each ROI.

A repeated-measures ANOVA comparing 3 factors, region (BA 45/47, BA 44 and BA 6) × identification (identified, unidentified) × repetition (primes/controls, targets) was then conducted. The results of the ROI analysis are depicted in Fig. 3. The ANOVA yielded a three way interaction between region, identification and repetition, $F = 10.56$, $p < 0.001$. As follow-up, ANOVAs were then conducted separately for the identified-prime and unidentified-prime conditions. For the identified-prime condition, no significant main effects for either ROI or repetition were found, F 's < 2.5, ns, however the interaction between repetition and region was significant, $F = 7.01$, $p < 0.01$. Paired t -tests indicated that IP-primes showed significantly greater activation than IP-targets only in BA 45/47, $t(16) = 2.24$, $p < 0.05$, but not in other ROIs, t 's < 1. For the unidentified-prime condition, there was a significant main effect for repetition, $F = 5.52$, $p < 0.05$, showing a general repetition suppression effect. The interaction effect was also significant $F = 4.03$, $p < 0.05$. Paired t -tests indicated that activation was significantly greater for UP-controls compared to UP-targets in BA 6, $t(16) = 3.54$, $p < 0.005$, with a trend towards significance in BA 44 ROI, $t(16) = 1.90$, $p = 0.076$, but not in BA 45/47 ROI, $t(16) = 1.31$, ns. These results confirmed our earlier findings suggesting that repetition suppression occurred only in the posterior left frontal cortex (BA 6) for primes and targets in the unidentified-prime condition, while repetition suppression in the identified-prime condition occurred in anterior LIFG (BA 45/47).

Discussion

The primary goal of the present study was to examine whether the processing of unidentified primes can facilitate later identification of the same words (repetition priming). The behavioral results showed that, indeed, unidentified primes produced a substantial priming effect, suggesting that partial (presumably mostly perceptual) processing of the primes without the ability to identify the word is sufficient to facilitate later identification of the same words. Interestingly, identified primes did not result in the same general priming effect, but instead showed a relationship between the original reading speed of the prime and the amount of facilitation in

Table 6
Brain regions exhibiting priming-related activation changes following unidentified primes, comparing targets to controls

Brain region	BA	Cluster size (voxels)	x	y	z	Z-score	
<i>Repetition suppression: UP-controls>UP-targets</i>							
Occipital/temporal lobes							
L	Mid. occipital	19	8	-33	-94	8	4.12
R	Inf. occipital	18	19	36	-88	-4	5.03
L	Fusiform/inf. temporal	37	13	-48	-58	-4	4.04
R	Fusiform/inf. temporal	37	8	45	-67	-4	4.04
R	Fusiform	20	22	42	-40	-10	5.39
R	Sup./mid. temporal	39	11	39	-64	26	4.57
Parietal lobes							
R	Precuneus	7/2	21	18	-61	50	4.35
L	Precuneus*						
R	Post. central	2	20	42	-31	38	4.96
Frontal lobes							
L	Precentral/SMA/mid. cingulate/postcentral/precuneus	6/32/7	1114	-15	-13	47	10.73
R	Precentral/mid. cingulate/SMA	6	353	18	-28	47	6.13
L	Sup. frontal	8	36	-12	44	41	4.59
R	Sup. frontal	6	29	18	17	62	4.85
R	Mid./sup. frontal/mid. cingulate	6/8/32	117	27	21	36	5.24
R	Ant. sup. med. frontal	10	30	15	56	14	7.01
R	Ant. IFG	45	13	36	32	11	4.61
Other regions							
L	Ant. hippocampus/amygdala	-	60	-30	-25	-13	5.57
R	Ant. hippocampus/amygdala	-	19	27	-10	-10	4.33
L	Hippocampus tail	-	30	-39	-40	8	5.01
L	Thalamus/basal ganglia	-	8	-15	-13	8	5.43
R	Thalamus	-	186	24	-25	26	6.37
R	Basal ganglia	-	14	24	-10	-1	4.61
<i>Repetition enhancement: UP-targets>UP-controls</i>							
N/A							

Only clusters with an extent of at least 5 voxels were listed. For all Z-scores, p 's < 0.001, uncorrected. BA = Brodmann's area; x, y and z coordinates in Talairach space; L = left; R = right; mid. = middle; sup. = superior; inf. = inferior; med. = medial; ant. = anterior; post. = posterior; IFG = inferior frontal gyrus; SMA = supplementary motor area. *: extended from the frontal cortex (see the first cluster in the frontal lobes).

reading speed when the word was presented again—the longer the RT for the prime, the greater the decrease in reading speed for the target. This finding is consistent with previous research demonstrating that the magnitude of behavioral priming effects increases with increasing difficulty, complexity and unfamiliarity of the task (Graf and Ryan, 1990; Ryan and Schnyer, 2007; Ostergaard, 1998, 1999).

The additional finding that identified primes with the shortest RTs showed a negative behavioral priming effect instead of positive priming is puzzling. To our knowledge, this effect has not been reported previously in the priming literature. One possible explanation of this result might be that participants responded to some of the shortest prime trials even before they actually identified the word. Unfortunately the word identification paradigm used in the present study did not allow us to monitor the correctness of responses. Another explanation is that the negative priming observed here simply reflects regression to the mean, such that the unusually fast RT items during the first presentation were more likely to have longer RTs that were closer to the mean of IP-targets on the second presentation, producing an artifactual negative priming effect. It will be interesting in future studies to determine the reliability of this effect and, if reliable, the fMRI repetition effects associated with it.

Despite the fact that positive behavioral priming was evident only for primes with relatively long RTs in the identified-prime

condition, significant repetition suppression effects were still found in several brain regions, including bilateral anterior IFG and bilateral middle temporal gyri, consistent with previous studies using similar paradigms. These findings suggest that fMRI signal may be a more sensitive measure of repetition effects than behavioral (RT) priming effects even when behavioral effects are subtle and difficult to detect. For example, Ryan and Schnyer (2007) observed repetition suppression effects in the absence of behavioral priming in one of their experimental conditions.

While the behavioral results from the unidentified-prime condition provide evidence that priming can occur based on partial processing of a prime, the fMRI activation results provide some clues as to the basis of this priming. In general, repetition suppression was observed in many regions involved in mirror reading, particularly posterior cortical regions that have been associated with perceptual processing of objects and also visually presented words, especially when presented in degraded or difficult conditions. For example, posterior inferior temporal and fusiform gyri have been associated with object identification and object priming (Buckner et al., 1998; Koutstaal et al., 2001; Wagner et al., 1997) and lexical/pre-lexical processing of visually presented words and lexical priming (Dehaene et al., 2002; Ryan and Schnyer, 2007; Poldrack and Gabrieli, 2001). Repetition suppression was also observed in parietal regions which may be related to mental rotation necessary

Table 7

Brain regions exhibiting priming-related activation changes following unidentified primes, comparing targets directly to their unidentified primes

Brain region	BA	Cluster size (voxels)	x	y	z	Z-score
<i>Repetition suppression: UP-primes>UP-targets</i>						
R	Mid./sup. temporal	17	60	-52	17	4.30
R	Mid. temporal	14	54	-40	2	4.31
<i>Repetition enhancement: UP-targets>UP-primes</i>						
L	Inf. occipital	19	5	-36	-79	4.08
L	Inf. occipital/lingual	17/18	39	-24	-97	4.11
R	Inf. occipital	19	6	45	-85	4.23
R	Inf. occipital	17/18	11	30	-100	4.34
L	Precuneus	7	8	-30	-61	4.09
L	Angular	39	8	-39	-73	4.32
L	Mid./sup. frontal	6/44/45	242	-24	32	5.79
R	Sup. frontal	8	22	27	26	4.38
L	Precentral/postcentral	6/4	29	-33	-28	4.31
L	Hippocampus tail	-	70	-36	-40	4.71
L	Mid. parahippocampal	-	7	-18	-34	4.25
R	Hippocampus	-	21	15	-19	4.85
R	Cerebellum	-	80	12	-61	6.00

Only clusters with an extent of at least 5 voxels were listed. For all Z-scores, p 's < 0.001, uncorrected. BA = Brodmann's area; x, y and z coordinates in Talairach space; L = left; R = right; mid. = middle; sup. = superior; inf. = inferior.

for reading words in mirror orientation (Cohen et al., 1996; Rypma et al., 1996).

Interestingly, although several regions of frontal cortex showed repetition suppression, this effect depended on whether or not the prime was identified. In particular, while repetition suppression was observed for the unidentified-prime condition in the posterior part of left precentral gyrus (BA 6), it was not present in the more anterior aspects of left inferior frontal gyrus (BA 45/47, 44), areas that were clearly activated during mirror reading in the present study. In contrast, items in the identified-prime condition showed repetition suppression in the anterior LIFG, but not in the more

posterior left frontal regions (BA 44, 6). Anterior LIFG has been implicated in the semantic analysis of format-invariant aspects of words (Petersen et al., 1988; Demb et al., 1995), while posterior LIFG and precentral gyrus are thought to be involved in transforming lexical information into phonological codes (e.g., Frost, 1998; Gold et al., 2005; Gold and Buckner, 2002), but not related to semantic processing (for review, see Poldrack et al., 1999). For example, Wagner et al. (2000) demonstrated that only anterior LIFG showed repetition suppression for repeated conceptual processes in a priming paradigm, but not when the items were initially processed perceptually. The present results are consistent

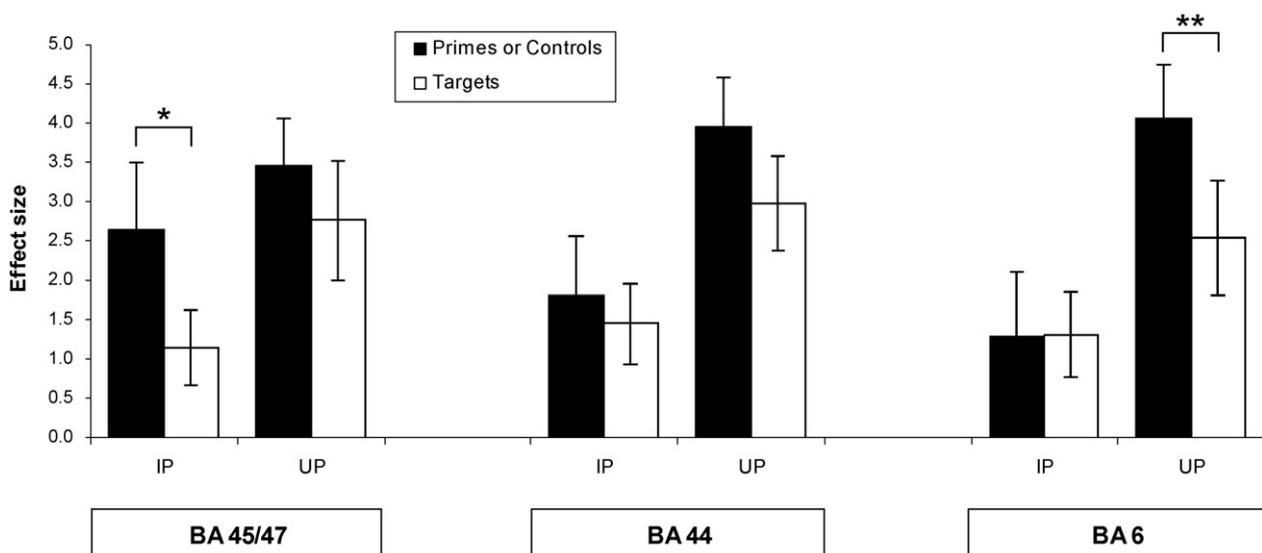


Fig. 3. ROI analyses of the repetition suppression effects in the identified-prime (IP) and unidentified-prime (UP) conditions in the three ROIs. The center coordinates of the ROIs are: BA 45/47: -39, 25, -16; BA 44: -48, 16, 21; BA 6: -50, -7, 36. In the identified-prime condition, the mean effect sizes of IP-primes and IP-targets across participants are shown. In the unidentified-prime condition, the mean effect sizes of UP-controls and UP-targets are shown. *: $p < 0.05$; **: $p < 0.005$.

with this notion. Priming for targets with identified primes showed repetition suppression in the anterior LIFG, presumably relying on the repetition of semantic processing of the word as a basis for subsequent priming. This finding replicates previous priming studies using the same mirror reading paradigm with identified primes in which repetition suppression was found in a similar region of the anterior LIFG (Poldrack and Gabrieli, 2001; Ryan and Schnyer, 2007). In both of those studies, items that were not identified during the first presentation were excluded from subsequent priming analyses.

Unidentified primes resulted in reduced activation only in posterior but not anterior left frontal cortical areas, presumably because the unidentified primes were processed perceptually without access to their meaning. Instead, participants likely relied primarily on phonological transformation of the re-oriented letters and syllables to try to “sound out” the words. This strategy of letter-by-letter reading utilizing phonology for identifying mirror words has been discussed elsewhere (Ryan et al., 2001). Therefore, when the previously unidentified primes were presented again, processes involved in phonological transformation were likely more efficient, reflected in reduced activation in the precentral gyrus (BA 6). Repetition suppression in the left middle temporal gyrus might also be reflecting a similar neural mechanism as others have postulated that this region may also mediate phonological code retrieval (Indefrey and Levelt, 2004). Taken together, the results are consistent with the idea that the basis for the priming in the unidentified-prime condition was primarily increased perceptual fluency rather than semantic processing and fits well within a component process view of priming (Henson, 2003).

According to the component process view one might also predict repetition suppression in the posterior left frontal cortex for words in the identified-prime condition, given that similar phonological processes should have been repeated for primes and targets. However, repetition suppression was evident only in the anterior LIFG (presumably mediating semantic processing) but not posterior left frontal regions. One explanation for this finding involves the emphasis of processing within a task that varies across stimuli. For example, although all mirror words likely share a common set of processes that are utilized during reading (letter rotation, phonological transformation, lexical access, access to semantic representations, etc.), the degree to which they are engaged likely depends on characteristics of the specific item that determine difficulty such as word length, ambiguity of rotated letters or similarity to other lexical items. Behavioral priming for repeated items may therefore be mediated by different processes, even within the same priming paradigm, and these differences may be mirrored in the magnitude of repetition suppression within brain regions mediating these processes. Mirror words in the unidentified-prime condition strongly emphasized aspects of perceptual processing such as letter rotation and phonological transformation, downplaying the importance of semantic processing and resulting in repetition suppression in regions mediating those perceptual processes. Consistent with this idea was the finding that control words in the unidentified-prime condition showed greater activations than their respective primes or controls in all three frontal ROIs (see Fig. 3), but this difference was disproportionately greater in the posterior left frontal region (BA 6) which may mediate phonological processing. On the other hand, identification of words in the identified-prime condition, where participants accessed the identity of the word relatively quickly, presumably engaged relatively less phonological analysis and emphasized instead the semantic analysis of the word, resulting in

repetition suppression within regions mediating semantic, but not perceptual, processing. Furthermore, this view would predict that repetition suppression within posterior LIFG should vary linearly with mirror reading difficulty, even when the item is identified. Thus, as the time taken to identify words in the identified-prime condition increases, more perceptual processing is necessary, and repetition suppression in this region should increase as well. Further studies are needed to determine whether this hypothesis is correct.

An alternative explanation of region-specific neural repetition suppression is the “response-learning hypothesis” (Dobbins et al., 2004). By this view, decision operations can be automated through repetition and may result in the complete bypassing of some of the previously engaged components via a learned association between object identity and the prior response, resulting in faster response times and neural repetition suppression effects. Indeed, the authors suggest that, at least in some priming conditions, automated decision operations might be the main source of repetition suppression. However, in our design, the unidentified-primes were not fully processed and no responses were actually made to these items. It cannot be the case that the response time facilitation for identifying targets was due to a learned association between the prime identity and the response since no decision was made regarding the prime and no motor response carried out. We cannot rule out the possibility that some component processes might be bypassed completely during repetition of primes and targets, but it is unlikely that these components involved the decision regarding identity of the prime and target, at least within the unidentified-prime condition. Further studies are necessary in order to identify whether processing of unidentified primes involves different strategies and component processes that may be omitted subsequently during the processing of their targets.

The present findings are also consistent with a recent imaging study using a lesion approach. Wig and colleagues (2005) applied transcranial magnetic stimulation (TMS) to disrupt processing in the anterior LIFG while participants were making living/nonliving judgments during the study phase of a priming experiment (note that participants were still able to identify the objects and make correct judgments) and then employed fMRI to determine how this would effect behavioral priming and repetition suppression when the primes were repeated. They found that disrupting anterior LIFG eliminated behavioral priming entirely and also eliminated the repetition suppression effects that were originally found in anterior LIFG and left middle temporal gyrus but had no impact on repetition suppression effects in the posterior cortical regions such as middle and inferior occipital gyri. Their results provide further evidence that disrupting neural processing of the primes in the anterior LIFG (presumably related to semantic processing), analogous to our unidentified primes, eliminates the repetition suppression effects in the semantic processing brain regions but not in the perceptual processing areas. Interestingly, when Wig et al. (2005) disrupted the semantic processing of the primes, behavioral priming was entirely eliminated, while the present study still resulted in a substantial behavioral priming effect in the unidentified-prime condition. One reason might be the choice of the priming task. Wig et al. (2005) used a semantic (living/non-living) judgment task that might rely more heavily on semantic processes, compared to mirror word identification task that is mediated primarily by perceptual analysis, and may be less affected by a disruption of semantic processing of the primes.

Repetition suppression in the unidentified-prime condition was also observed in bilateral anterior medial temporal lobes and a cluster in the left posterior hippocampus. Although less common,

similar findings have been reported in several priming studies (e.g., Experiment D in Henson et al., 2003; O’Kane et al., 2005). Repetition suppression in anterior MTL (including perirhinal cortex and possibly anterior hippocampus) is usually thought to be related to a familiarity signal (i.e. repeated stimuli showing reduced activation relative to new stimuli), although it is still under debate whether this signal change indicates “perceived” or “true” familiarity (Daselaar and colleagues, 2006). Henson and colleagues (2003) noted that this signal reduction may not depend upon whether or not recognition of the item actually occurred. An alternative view is that anterior MTL signal reduction might reflect less encoding because the items are repeated (the “novelty encoding hypothesis”, Tulving et al., 1996; Habib et al., 2003). By this view, novel items will trigger more extensive memory encoding processing which is mediated by anterior MTL. Therefore, repeated items should show reduced neural activations compared to unrepeated items. The exact role of repetition suppression in anterior MTL found in priming paradigms is still unclear and requires further examination.

As discussed earlier, extensive repetition suppression effects were observed in the unidentified-prime condition when comparing targets to the unprimed baseline control words. In contrast, when directly comparing repeated targets to their unidentified primes, an opposite pattern was observed — repetition enhancement effects were found in several brain regions involved in mirror reading, but only two small regions showed repetition suppression. According to the component process view, this may reflect more intensive and perhaps additional processing operations required for the identification of targets, compared to the incomplete processing of their primes, even though some parts of the perceptual process might become more efficient after repetition.

Repetition enhancement has been reported in at least two other imaging studies using unidentified stimuli (Dolan et al., 1997; see also George et al., 1999). In Dolan et al. (1997), participants viewed binarized black and white images of either faces or objects, which were difficult to classify on their initial presentation (only 13% of object images and 55% of face images were classified correctly; the remainder were therefore “unidentified”). When these degraded images were repeated following intervening presentation of an intact version of each image, classification rates increased substantially (87% for objects and 93% for faces). When comparing initial presentations (mostly unidentified) to their repetitions (mostly identified), repetition enhancement was observed in left fusiform gyrus for objects and right fusiform gyrus for faces.

The study by Dolan et al. (1997) yielded similar repetition enhancement results as our comparison of unidentified primes versus their targets, but differs from the present study in one critical aspect: they pooled both identified and unidentified trials in their primed and unprimed conditions (similar to the methods in George et al., 1999), and therefore the imaging results were influenced by a mixture of effects arising from both identified and unidentified trials. The present study allowed us to separate these effects and also compare changes in activation between unidentified-primes and their targets that result in repetition enhancement (when targets are compared to the unidentified primes directly) and repetition suppression (when targets are compared to similar, but unprimed, stimuli). Consistent with the predictions of the component process view, the present results suggest that the identification of these repeated targets indeed required additional processing compared to the incomplete processing of their unidentified primes, but they were still processed more efficiently than unprimed control items.

Conclusion

In summary, the present study demonstrates that, even when a mirror word prime is not identified initially, the perceptual processing engaged during initial presentation is sufficient to produce substantial behavioral priming, accompanied by repetition suppression effects in brain regions that mediate perceptual, but not semantic or conceptual, processing. These findings are consistent with the general behavioral predictions of a TAP view of priming, and more specifically, with the neural predictions provided by a component process priming theory. Our results strengthen previous findings in the literature suggesting that priming may be mediated by both “bottom-up” and “top-down” processing of the stimuli. They may work in parallel, but may also interact with each other, depending upon the specific circumstances of the priming test. We suggest that recent exposure to the perceptual processes is sufficient to prime later identical perceptual processes of the same repeated stimuli. Furthermore, recent exposure to the presentation of a stimulus in any form that fully engages its semantic representation will prime all aspects of its repeated presentation, semantic and perceptual. Increasing the efficiency of semantic processing will serve to disambiguate the perceptual processing of the unfamiliar item as analysis progresses, and this effect will be particularly evident when the task is unfamiliar or difficult. It remains for further investigations to determine how these two types of priming interact with each other.

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