

Brain Activation during Masked and Unmasked Semantic Priming: Commonalities and Differences

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Abstract

■ Using fMRI during a lexical decision task, we investigated the neural correlates of semantic priming under masked and unmasked prime presentation conditions in a repeated measurement design of the same group of 24 participants (14 women). The task was to discriminate between pseudowords and words. Masked and unmasked prime words differed in their degree of semantic relatedness with target stimuli. Neural correlates of priming were defined as significantly different neural activations upon semantically unrelated minus related trials. Left fusiform gyrus, left posterior inferior frontal gyrus, and bilateral pre-SMA showed priming effects independent of the masking condition. By contrast, bilateral superior temporal gyri, superior parietal lobules, and the SMA proper demonstrated greater neural

priming in the unmasked compared with the masked condition. The inverted contrast (masked priming minus unmasked priming) did not show significant differences even at lowered thresholds of significance. The conjoint effects of priming in the left fusiform gyrus suggest its involvement as a direct consequence of the neural organization of semantic memory. Activity in brain regions showing significantly more neural priming in the unmasked condition possibly reflected participants' evaluation of the prime–target relationship, presumably in the context of semantic matching. The present results therefore indicate that masked and unmasked semantic priming partially depend on dissociable mechanisms at the neural and most likely also at the functional level. ■

INTRODUCTION

Semantic processes during language comprehension have been frequently investigated with the primed lexical decision task (LDT) in behavioral (e.g., Meyer & Schvaneveldt, 1971), electrophysiological (e.g., Kiefer, Weisbrod, Kern, Maier, & Spitzer, 1998), and neuroimaging studies (e.g., Kotz, Cappa, von Cramon, & Friederici, 2002). In this paradigm, a prime word is presented first, which is then replaced by a target upon which participants are forced to decide whether or not the target is an existing word. Variants of this paradigm incorporate at least three conditions. Whereas the prime is always a real word, the target can either be a real word or a pseudoword, with the latter having a similar appearance as a word but is actually not existing in the real world. When the target is an existing word, its semantic meaning can either be related (R) or unrelated (U) to the meaning of the prime. As a typical outcome, decisions on semantically related targets are usually faster and less error prone compared with the unrelated condition, a phenomenon called “semantic priming” (see Neely, 1991, for a review).

Several mechanisms have been discussed to explain semantic priming effects within LDTs. One mechanism involves the level of semantic representations. Semantic memory can be conceived of as a widely distributed neu-

ronal network where specific cell assemblies code specific semantic features and where specific feature modalities are associated with activations of specific brain regions (Kiefer & Pulvermüller, 2012; Martin & Chao, 2001; Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995; Plaut, 1995; Warrington & Shallice, 1984). In this framework, a given concept spans a subspace of features of visual, auditory, and other modalities. When these features are activated, a so-called “semantic field” emerges (Jung-Beeman, 2005), and the meaning of a word can be accessed (Plaut, 1995). Because of the timing schedule in a typical priming experiment, the target stimulus is presented while the meaning of the prime is still activated within neural networks coding semantic information. If the features associated with the target overlap with those of the prime, the neuronal network needs less time to represent the meaning of the target word (Plaut, 1995) and the lexical decision on the related target can be given faster. It is assumed that preactivation of semantic features can occur automatically and is not linked to prime awareness.

Other priming mechanisms are assumed to depend on strategic stimulus processing and are consequently associated with conscious prime perception. “Expectancy generation” is a mechanism that refers to the generation of a set of potential related target words after processing the prime (Neely, Keefe, & Ross, 1989; Posner & Snyder, 1975). If the target is one of the generated candidates as might be the case in the related condition, the lexical

decision can be given faster. However, the observation of relatedness proportion effects on masked semantic priming have promoted the notion of an episodic account of priming according to which the prime event creates a memory resource, which facilitates target recognition even when the primes are presented unconsciously (e.g., Bodner & Masson, 2003).

“Semantic matching” (Neely et al., 1989; Lupker, 1984; Neely, 1977) refers to a process in which the meaning of the target is compared with that of the prime. In cases where the prime is a real word, a positive match implies that the target must also be a real word, thereby facilitating the lexical decision on semantically related targets while relatively more time is spent on processing unrelated targets and pseudowords.

As mentioned above, a prerequisite to strategic mechanisms is the prime’s association with consciousness. Particularly, expectancy generation can only be applied if there is sufficient time between prime and target (but see Bodner & Masson, 2003). A prime–target SOA smaller than 300 msec (Neely, 1991) or 200 msec (Altarriba & Basnight-Brown, 2007) is generally assumed to preclude semantic matching and expectancy generation. For expectancy generation, however, SOAs even greater than 500 msec appear necessary (Chwilla, Hagoort, & Brown, 1998). It is conceivable that semantic matching can be performed at much shorter SOAs because meanings of the prime and the target may have already been processed, so that only their relation remains to be processed. There is evidence that semantic matching can operate at SOAs as short as 165 msec (Koivisto, 1998). However, even at those short SOAs, priming effects may be modulated by strategic processes when primes are consciously perceptible (Kiefer, 2002; Naccache & Dehaene, 2001; Kiefer & Spitzer, 2000).

To assess automatic priming processes in isolation without possible contamination of strategic processes, conscious perception of the primes can be prevented by using masking techniques (Breitmeyer, 2007), which render the use of strategies rather unlikely (Henson, 2003; Merikle, Joordens, & Stolz, 1995), while typical priming effects still occur. Although masked priming had a smaller magnitude than unmasked priming (Kiefer, 2002; Kiefer & Spitzer, 2000), these subliminal masked priming effects demonstrate that semantic word meaning can be accessed automatically in an unconscious fashion (Adams & Kiefer, 2012; Kiefer & Martens, 2010; Kiefer & Brendel, 2006; Marcel, 1983). In ERP studies (Martens, Ansorge, & Kiefer, 2011; Kiefer & Martens, 2010; Kiefer & Brendel, 2006; Kiefer, 2002; Kiefer & Spitzer, 2000) that are ideal to capture fast-decaying subliminal processes because of their high temporal resolution, masked and unmasked priming modulated the N400 ERP component, an index of semantic processing. The comparable topography of priming effects in the masked and unmasked conditions suggests that the underlying neural generators are similar. Intracranial recordings (Nobre & McCarthy, 1995) and source analyses of scalp potentials (Kiefer, Sim, Helbig, & Graf, 2011; Kiefer,

Schuch, Schenck, & Fiedler, 2007) indicated a contribution of ventral temporal areas including the fusiform gyrus (FFG) to the generation of the N400 ERP component. However, masked N400 priming effects were only observed at very short SOAs (67 msec) and decayed at a longer SOA of 200 msec, whereas magnitude of unmasked N400 priming increased as a function of SOA (Kiefer & Brendel, 2006; Kiefer & Spitzer, 2000), presumably because of a more effective engagement of strategic processes in the visible condition at longer SOAs.

The neural substrate of masked and unmasked semantic priming can be determined with a high spatial resolution in fMRI studies. Previous studies mainly investigated the neural correlates of supraliminal priming where both the prime and the target are accessible to consciousness. For visible primes, usually greater brain activation for unrelated than for related trials was found (but see Raposo, Moss, Stamatakis, & Tyler, 2006), a pattern that we refer to as neural priming in analogy to behavioral priming effects. Probably owing to differences in experimental design (particularly visual vs. auditory stimulation, SOAs), data analysis, and thresholding the brain activation maps, the neural substrate associated with priming varies widely across studies. Brain regions that have been reported to associate with unmasked supraliminal priming include the inferior frontal gyrus (IFG; Wible et al., 2006; Matsumoto, Iidaka, Haneda, Okada, & Sadato, 2005; Wheatley, Weisberg, Beauchamp, & Martin, 2005; Giesbrecht, Camblin, & Swaab, 2004; Copland et al., 2003; Kotz et al., 2002), anterior insula/deep frontal operculum (Kotz et al., 2002), middle frontal gyrus (MFG; Giesbrecht et al., 2004; Rissman, Eliassen, & Blumstein, 2003; Kotz et al., 2002), anterior cingulate gyrus (Wible et al., 2006; Matsumoto et al., 2005), inferior parietal lobule (Giesbrecht et al., 2004), middle temporal gyrus (MTG; Gold et al., 2006; Giesbrecht et al., 2004; Copland et al., 2003), superior temporal gyrus (STG)/temporal plane (Wible et al., 2006; Matsumoto et al., 2005; Rissman et al., 2003; Kotz et al., 2002), and FFG (Gold et al., 2006; Wible et al., 2006; Wheatley et al., 2005). On the basis of the assumption that conceptual features are grounded in brain regions involved in stimulus perception and encoding (Kiefer & Barsalou, 2013; Kiefer & Pulvermüller, 2012; Martin, 2007; Barsalou, Kyle Simmons, Barbey, & Wilson, 2003), priming in the FFG appears particularly interesting because it relates to semantic processing in its strict sense as opposed to complementary strategic processing (Wheatley et al., 2005). Nevertheless, because primes were always consciously perceptible in the aforementioned studies, it is likely that strategic processes also contributed to the priming effects observed (Kiefer, 2002; Naccache & Dehaene, 2001).

In contrast to these robust semantic priming effects obtained with visible primes in previous neuroimaging studies, evidence on the neural correlates of masked semantic priming is scarce and inconclusive. In one study by Devlin, Jamison, Matthews, and Gonnerman (2004), semantic priming was reported in the left MTG and bilateral

angular gyri whereas the FFG did not demonstrate a priming effect. Furthermore, semantic priming was not significant at the behavioral level. Other studies did not observe masked semantic priming effects at the behavioral and the neural level (Kherif, Josse, & Price, 2011; Devlin, Jamison, Gonnerman, & Matthews, 2006). In particular, it is open whether semantic priming with visible and with unconsciously perceived masked primes involve the same brain regions.

Although priming is most commonly associated with larger activity in the unrelated compared with the related condition, in some instances an increased fMRI signal in the unrelated priming condition has been found, in particular during masked repetition priming (Schnyer, Ryan, Trouard, & Forster, 2002). This signal increase as a function of masked repetition priming has been explained by a superposition of activity elicited by the prime and the target in brain regions associated with word identification (Schnyer et al., 2002). However, as our priming paradigm (see below) involves only semantically related and unrelated prime target pairs, we expected a reduction of the fMRI signal as a function of semantic relatedness.

In summary, different studies have reported varying sets of brain regions during unmasked semantic priming. Although it has been acknowledged that the observed priming effects may possibly reflect controlled strategic processing in addition to rather automatic semantic processes (Wheatley et al., 2005; Copland et al., 2003), none of the previous studies has investigated masked and unmasked semantic priming in a within-subject design. Therefore, we conducted an fMRI study comparing the effects of masked and unmasked semantic priming in the same set of participants. We hypothesized that brain regions showing conjoint priming effects irrespective of the masking condition may support processing of semantic features, which are automatically activated by the prime even under unconscious viewing conditions. We expected these conjoint priming effects to be located in posterior brain regions, particularly in the FFG. In case of additional strategic processes in service of evaluating the semantic relationship between prime and target (semantic matching), we expected recruitment of additional brain regions when contrasting unmasked minus masked priming.

METHODS

Participants

Twenty-four students (14 women) aged 22.3 years on average ($SD = 1.7$ years) were recruited from the local university and were paid € 30 for participation. All of them were German native speakers and right-handed as assessed with the Edinburgh Inventory (Oldfield, 1971). Neither psychiatric nor neurological diseases nor any contraindications regarding the fMRI procedure were reported. Written informed consent was obtained before the experiment. The study was approved by the local

ethical committee at the Ulm University and was in accordance with the Declaration of Helsinki.

Stimuli

Stimuli were taken from previous studies conducted by our group (Kiefer & Martens, 2010; Kiefer, 2002; Kiefer & Spitzer, 2000) consisting of German words (nouns, verbs, adjectives) and pronounceable pseudowords, with the latter having been derived from regular German words by changing one or two letters to make them meaningless. Parallel stimulus lists were created, each containing 30 word–word pairs related in meaning (R), 30 word–word pairs unrelated in meaning (U), and 60 word–pseudoword pairs (P). The first word of each pair was later used as prime and the second item as target. Stimuli were matched for average word length and frequency (Ruoff, 1990) across and within lists [list-by-event type-by-prime/target ANOVAs: word length: $F(17, 702) = 0.03, p = 1$, post hoc Fisher LSD tests: all $p > .70$; word frequency (R and U only): $F(14, 525) = 0.003, p = 1$, post hoc Fisher LSD tests: all $p > .93$].

Different from the experimental lists, 20 R, 20 U, and 40 P pairs (not matched) were used to form two practice runs with 10 R, 10 U, 20 P pairs each. All stimuli were unique, that is, there were no repetitions across primes and targets within and across lists.

An initial setup of trial ordering and trial onsets with respect to fMRI repetition time (TR) was based on the program Optseq2 (surfer.nmr.mgh.harvard.edu/optseq/; see also Dale, 1999). Ordering of trial type was pseudo-randomized such that a specific trial type did not appear more than three times in direct succession. Onsets were jittered by randomly adding fractions of the TR. Average trial onset asynchronies were 24.0 sec for R trials, 23.8 sec for U trials, and 12.3 sec for P trials. Average trial onset asynchronies of R and U trials did not differ, $t(56) = 0.029, p = .98$.

Visual stimulation and recording of RTs (starting from target onset) was performed using Experimental Run Time System 3.35 (BeriSoft Cooperation, Frankfurt/Main, Germany) running on a standard PC. Stimuli appeared on MRI-compatible video goggles (VisuaStim Digital, Resonance Technology Inc., Northridge, CA, USA). If necessary, correction lenses were provided to ensure sufficient visual acuity. Resolution was set to 800×600 pixels, and screen refresh frequency was set to 60 Hz (frame duration = 16.67 msec; stimulus presentation and screen refreshes were synchronized). In the run-up to the study, it was checked that the goggles were sufficient for presenting stimuli as short as 33 msec, which was the duration to present the primes and the backward masks in the masked condition. Stimuli appeared in white 24-point IBM8BIT font against black background in the center of the display and spanned a visual angle of 1.0° vertically and, depending on word length, 1.4° – 5.7° horizontally. All primes and targets were held in lowercase except

for the first letter of nouns and of pseudonouns to conform to German orthography.

Procedure

Participants performed a primed visual LDT (Meyer & Schvaneveldt, 1971) in two versions. In the masked version, a forward pattern mask consisting of 10 randomly drawn upper case letters was shown for 133 msec in the middle of the screen. After disappearance of the mask, a prime word was presented for 33 msec. The prime was replaced by a backward pattern mask lasting 33 msec, created in the same way as the forward mask, although it was not identical to that. Then the target was presented with duration of 500 msec, resulting in a prime–target SOA of 67 msec. Participants were asked to decide whether or not the target was a German word and to indicate their decision by pressing the left or the right button of a self-built MRI-compatible keyboard with their right index or middle finger, respectively. The response was to be given within a time window of 2000 msec beginning with target onset. After offset of the target a black background was presented for 1500 msec. Responses were instructed to be given as fast and as accurate as possible, and participants were not informed about the presence of the masked prime. Instead, they were prepared to only see a “random letter string” lasting for 200 msec before target presentation. The overall trial duration was fixed to 2200 msec. During the intertrial interval, a screen centered crosshair was shown, which participants were asked to fixate. They were also sensitized for the variability of the intertrial interval (mean = 3.9 sec, maximum = 25.4 sec) and instructed to focus on the fixation cross in order not to miss the onset of the next trial. At the beginning and at the end of the fMRI session, the fixation cross was shown for 13.2 and 22 sec, respectively, to account for scanner equilibration and to capture the hemodynamic response associated with the last trial.

In the unmasked condition, no masks were used. Instead prime duration was 200 msec to render the primes clearly visible. The prime was immediately followed by target presentation. The remaining trial structure was identical to the masked priming condition described above.

After the experimental session still inside the scanner but off-line, an additional task was performed to test the visibility of the primes presented in the masked priming condition (Kiefer, 2002). For this task, in half of the trials a word (33 msec) appeared that had originally been used as prime in the masked priming condition. During the other half of the trials, a letter string consisting of seven repetitions of a randomly drawn upper case letter (33 msec) was shown. In both cases the stimulus was presented between a forward mask (133 msec) and a backward mask (33 msec), consisting of 10 different randomly drawn upper case letters as in the main experiment. The second item of a trial was always a word (no pseudowords) taken from the main experiment but no response had to be given here.

This context word was presented at the position of the lexical decision target in the main experiment to keep stimulation comparable. Participants were told to concentrate on the masks and to indicate by button press whether the masks contained a word (right index finger) or a repeated letter string (right middle finger). Emphasis was on accuracy over speed. Execution of this task was self-paced to ascertain that participants felt optimally prepared before starting each trial. The visibility test comprised 80 trials: 40 word trials (20 R, 20 U primes randomly selected from the masked condition) and 40 repeated letter string trials. Trials were presented in random order. Just before the test, participants had to undergo 10 practice trials (six word trials, four letter string trials).

Before the main experiment, participants were carefully instructed. In the scanner, participants laid supine, with their head resting in foam padding to reduce head movements. The masked and the unmasked versions of the paradigm were performed in two separate fMRI sessions. Session order and stimulus lists were counterbalanced across participants. Before each run, participants had to complete a practice run (10 × R, 10 × U, 20 × P), with the trial structure being nearly identical to the upcoming task. The only difference was inclusion of visual feedback after each trial (“correct,” “wrong,” and “faster!” in red font). The scanning session ended with acquisition of a T1 weighted structural image of the brain. After scanning, participants were informed about the presence of the primes in the masked condition and were asked if they had perceived those primes or if they had recognized that the random letter strings flickered.

MRI Data Acquisition

Functional images were acquired on a 3-T magnetic resonance scanner (Magnetom Allegra, Siemens AG, Erlangen, Germany) in combination with a single channel transmit/receive head coil (RAPID Biomedical GmbH, Rimpar, Germany). During the experimental runs, an echo-planar pulse sequence (EPI) was applied to measure the T2*-weighted BOLD signal. The following parameters were used: TR = 2200 msec, echo time = 39 msec, flip angle = 90°, field of view = 230 mm, matrix size = 64 × 64, number of slices = 34, slice thickness = 3.0 mm, interslice gap = 0.6 mm, isotropic voxel size of 3.6 mm³. Ascending slice acquisition was parallel to a tangent plane touching the inferior surfaces of the OFC and the cerebellum. Scan time per experimental run was 774 sec, corresponding to 350 EPI volumes. To obtain a high-resolution T1-weighted structural image for later coregistration purposes, a magnetization prepared rapid acquisition gradient-echo sequence was employed (TR = 2080 msec, echo time = 3.93 msec, inversion time = 1100 msec, flip angle = 12°, field of view = 256 mm, matrix size = 256 × 256, voxel volume = 1 mm³, slice orientation: sagittal, scan time = 467 sec).

Data Analysis

Behavioral Data

Responses obtained from the LDT were analyzed for RTs and errors. Pseudoword trials were of no interest and not further analyzed. Individual mean RT data for R and U trials were fed into a 2×2 repeated-measures ANOVA with factors Masking (masked vs. unmasked) and Semantic relatedness (R vs. U). A second ANOVA was performed on rates of erroneous responses calculated as the percentage of incorrect responses per trial type.

From the responses given in the prime visibility test, d' (Green & Swets, 1966) was calculated by transforming the false alarm rate for words (collapsed across R and U primes) into a z -score, which was subtracted from the z -score pertaining to the hit rate. The subject-wise d' values were tested for significant deviation from zero using a one sample t test.

All significance levels were set to a level of $p < .05$.

MRI Data

Imaging data preprocessing and statistical analyses were performed with Statistical Parametric Mapping (SPM8, Wellcome Department of Cognitive Neurology, London, UK). Preprocessing started with slice timing correction and spatial realignment of the EPIs of each session to the session mean. Afterward, images of each session were aligned to each other by coregistering the two mean EPIs and applying the resulting parameters to the images of the second session (either masked or unmasked because of counterbalancing). Thereafter, the individual T1 image was coregistered to the mean EPI of the first run. The T1 image was then segmented into gray and white matter, which was the input to the spatial normalization procedure realized by the DARTEL process stream (Ashburner, 2007). Individual EPI series were transformed into standard Montreal Neurological Institute (MNI) space and resliced to a spatial resolution of isotropic 2 mm^3 . Finally, experimental EPI time series were smoothed using a Gaussian kernel with 8 mm FWHM.

After data preprocessing, a hierarchical standard modeling approach was used. For each participant a session separated GLM model was set up with onsets for each condition of correct R, U, and P trials. As conditions of no interest, onsets of incorrect decisions were added to the design matrix as were the spatial realignment parameters. Resulting stick functions were convolved with the canonical hemodynamic response function and its time derivative. To remove low-frequency scanner drifts, data were high-pass filtered with a frequency cutoff at 128 sec, and an autoregression model of polynomial order 1 was used to account for temporally correlated residual errors. Upon model estimation, contrast images representing the main effects “canonical R > implicit baseline” and “canonical U > implicit baseline” were created for both masking conditions and propagated to a random-effects analysis, implemented as flexible factorial design. The interaction masking by relat-

edness was specified as a single factor with four levels (R_{masked} , U_{masked} , R_{unmasked} , U_{unmasked}) by concatenating the two underlying factors. A second factor modeled the subject-related variance. After estimation, two one-sided t contrasts were computed to test for significant neural semantic priming per each masking condition [$(U_{\text{masked}} \text{ minus } R_{\text{masked}})$, $(U_{\text{unmasked}} \text{ minus } R_{\text{unmasked}})$]. The statistical parametric maps were each thresholded at $p < .005$ at the voxel level in combination with a cluster extent threshold that required cluster sizes of contiguously significant voxels to survive a level of $p < .05$, corrected for multiple comparisons using the topographical false discovery rate (FDR) correction method (Chumbley & Friston, 2009). This corresponded to cluster extent thresholds of $k = 337$ voxels. The two contrasts were used for a conjunction analysis (using SPM8's ImCalc function) to test for conjointly significant voxels demonstrating priming in the masked and unmasked condition. No further correction in terms of a cluster extent threshold had to be applied here because the statistical parametric maps representing the input to the ImCalc procedure had already been thresholded before. Differences between the masked and the unmasked condition were computed by setting up two one-sided t contrasts modeling the interaction between factors masking condition (masked, unmasked) and semantic relatedness (R, U) to test for significantly greater priming activation in the unmasked versus the masked condition [$(U_{\text{unmasked}} \text{ minus } R_{\text{unmasked}}) \text{ minus } (U_{\text{masked}} \text{ minus } R_{\text{masked}})$] and vice versa [$(U_{\text{masked}} \text{ minus } R_{\text{masked}}) \text{ minus } (U_{\text{unmasked}} \text{ minus } R_{\text{unmasked}})$]. The statistical parametric maps pertaining to the interaction contrasts were thresholded at $p < .005$ at the voxel level combined with a cluster extent threshold of $p < .05$ corrected for multiple comparisons using the topographical FDR correction approach (Chumbley & Friston, 2009), corresponding to $k = 452$ voxels.

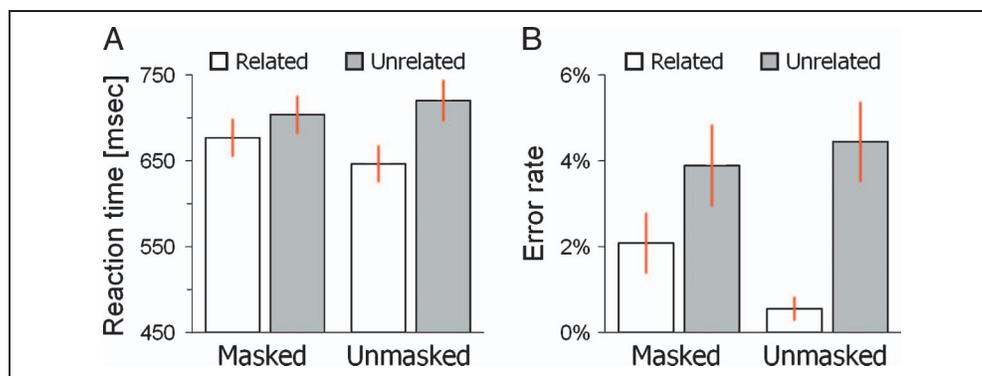
RESULTS

Behavioral

Averaged error rates across R and U trials were 3.0% in the masked and 2.5% in the unmasked condition. This difference was not significant, $t(23) = 0.63$, $p = .53$.

An ANOVA performed on correct RTs revealed significant semantic priming, that is, faster responses to related than unrelated targets (see Figure 1A; main effect of Relatedness, $F(1, 23) = 106.91$, $p < .001$). The interaction between Masking and Relatedness was also significant, $F(1, 23) = 23.91$, $p < .001$, reflecting less priming in the masked (U-R difference: 27 msec) than in the unmasked condition (74 msec). Post hoc tests (Newman-Keuls, nominal level of alpha, $p < .05$) showed that RTs on unrelated trials were significantly greater than on related trials under both masking conditions. A priming effect was also found for error rates (Figure 1B; main effect of relatedness, 1.3% (R) vs. 4.2% (U), $F(1, 23) = 13.32$, $p < .005$), whereas the Masking \times Relatedness interaction did not reach significance, $F(1, 23) = 2.12$, $p > .15$.

Figure 1. Behavioral results associated with the related and unrelated condition obtained from the masked and the unmasked priming condition. (A) Mean RTs. (B) Mean error rates. Error bars indicate *SEM*.



With regard to prime visibility, only two participants stated that they had been able to consciously perceive about two and five primes, respectively. Furthermore, eight participants reported to have recognized a flicker of the random letter string (i.e., the masks/prime). The objective test on prime visibility revealed a mean overall hit rate across words and repeated letter strings of 50.5% (range = 42.5–61.3%), which did not significantly differ from chance, $t(23) = 0.46$, $p > .65$. The critical measure of prime visibility, d' , was 0.02 on average (range: -0.39 to $+0.57$) and did not significantly deviate from zero,

$t(23) = 0.34$, $p > .73$. This strongly indicates that our masking procedure was successful in rendering the prime words inaccessible to conscious processing.

fMRI Data

Brain Regions Showing Conjoint Masked and Unmasked Semantic Priming

The conjunction of significant masked and unmasked priming [(U_{masked} minus R_{masked}) and (U_{unmasked} minus R_{unmasked})] yielded a set of brain regions, summarized in

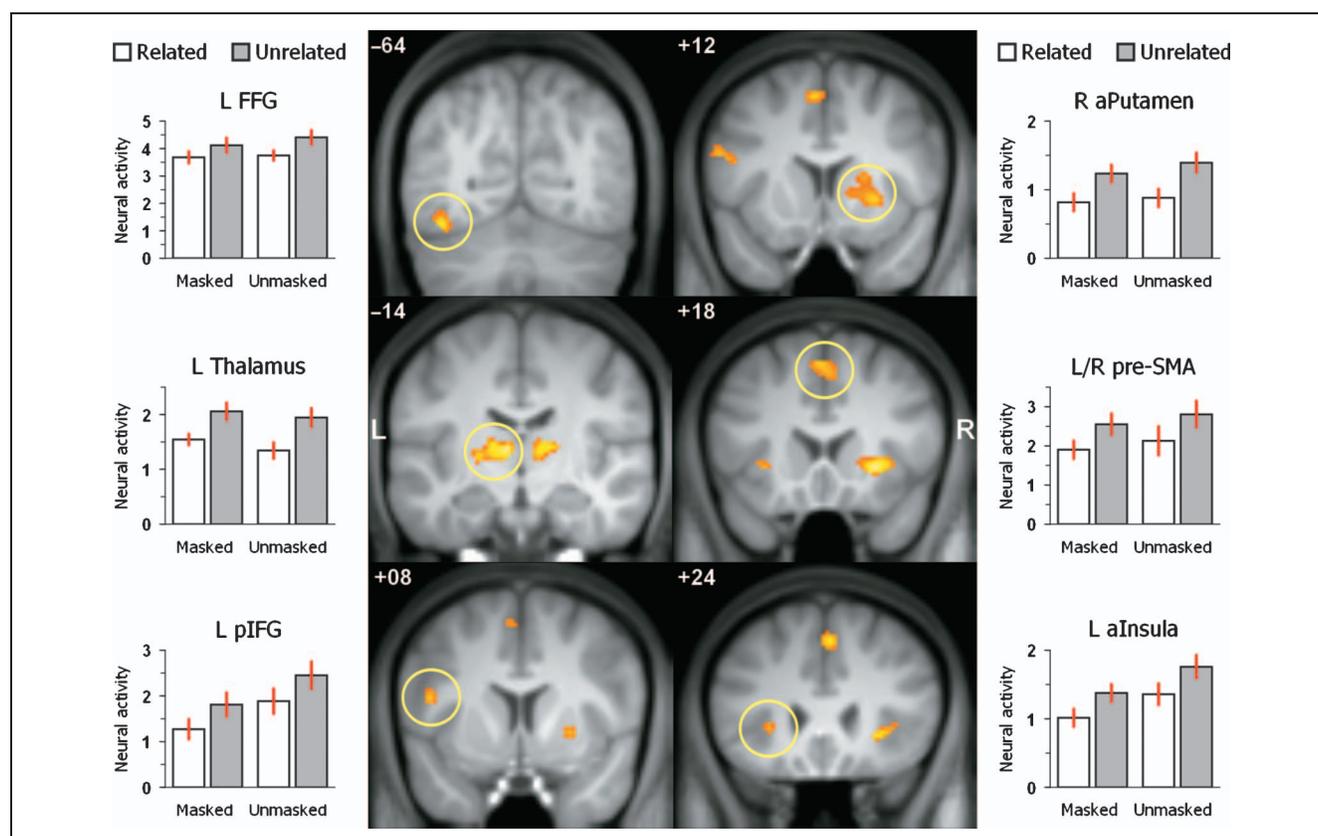


Figure 2. The two middle columns show the spatial conjunction of the contrasts masked semantic priming and unmasked semantic priming. Conjoint effects were overlaid on coronal sections of the group averaged T1 image. Numbers in white color denote the y coordinates of the slices in MNI space. The left and right columns depict magnitude of neural activation, as represented by averaged parameter estimates associated with related and unrelated trials under masked and unmasked prime conditions. Yellow circles indicate where the parameter estimates were extracted from. Error bars represent *SEM*. L = left; R = right; aInsula = anterior insula; aPutamen = anterior putamen.

Table 1. Brain Regions Showing Semantic Priming in Both the Masked and the Unmasked Condition

	Region	BA	Number of Voxels	Peak Voxel			
				x	y	z	z Score
L	FFG	19	101	-40	-66	-14	3.58
L	FFG	37		-36	-54	-8	2.98
L	MTG	37	14	-52	-60	0	2.84
L	Pre-SMA	6	174	-2	16	52	3.39
R	Medial superior frontal gyrus	8		4	22	46	3.73
L	IFG opercular part	44	65	-46	8	16	3.16
L	IFG opercular part	44		-54	12	22	3.04
L	Anterior insula	-	48	-30	18	-2	3.07
L	Anterior insula	-		-28	30	0	3.04
L	Thalamus	-	510	-8	-16	6	4.16
L	Thalamus	-		-20	-12	4	3.29
R	Thalamus	-	245	10	-12	6	3.97
R	Thalamus	-		16	-18	10	3.40
L	Putamen	-	14	-18	4	12	2.95
R	Anterior insula	-	307	28	16	-2	4.13
R	Putamen	-		22	12	10	2.98
L	Cerebellum	-	200	-8	-72	-26	3.60
R	Cerebellum	-		2	-68	-20	2.82
R	Cerebellum	-	45	14	-74	-34	3.01

The z scores were converted from t values by SPM8.

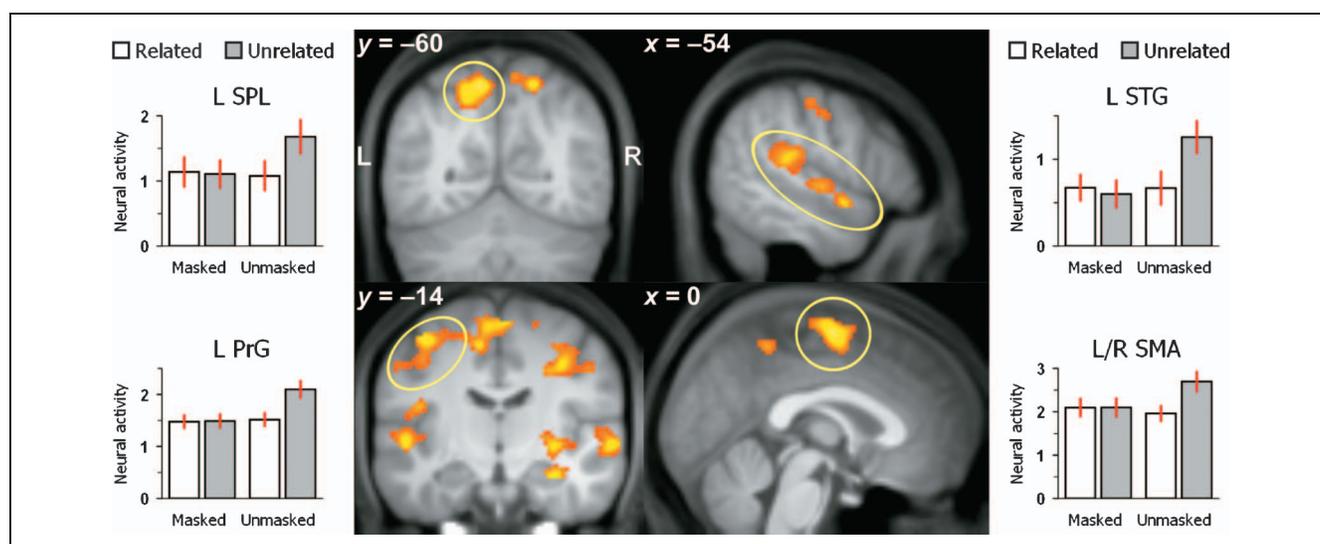


Figure 3. The two middle columns show the interaction contrast examining greater priming in the unmasked than in the masked condition, superimposed on coronal and sagittal sections of the group averaged T1 image. Coordinates refer to MNI space. The left and right columns depict cluster averaged parameter estimates associated with related and unrelated trials under masked and unmasked prime conditions. Yellow circles indicate where the parameter estimates were extracted from. Error bars represent SEM. L = left; R = right; PrG = precentral gyrus; SMA = SMA proper.

Figure 2 and Table 1. One cluster was located in the left FFG (BA 19/37; y range = -72 to -52). In its vicinity, the left posterior MTG (pMTG, BA 37) was also differentially activated by R and U trials in both masking conditions. Frontally, significant clusters emerged in the bilateral pre-SMA (BA 6) and in the left posterior IFG (pIFG; opercular part, BA 44). The pattern was also found in the anterior insula, bilaterally. In the right hemisphere the cluster extended from the anterior insula into the anterior putamen. Conjoint neural priming effects were furthermore observed in the bilateral thalami and the cerebellar hemispheres.

Differences between Masked and Unmasked Semantic Priming

Brain regions bearing an effect of significantly greater unmasked than masked neural priming [$(U_{\text{unmasked}} \text{ minus } R_{\text{unmasked}}) \text{ minus } (U_{\text{masked}} \text{ minus } R_{\text{masked}})$] are summarized in Figure 3 and Table 2. The effect was very prominent along

the bilateral STG (BA 22/41/42; y range = -44 to $+4$). Another significant cluster spread from the bilateral superior parietal lobules (SPL, BA 7) and adjacent aspects of the precuneus (BA 5) into the left postcentral (PoG, BA 3) and precentral gyri (BA 6), from where it extended into the bilateral SMA proper (BA 6), including small aspects of the left middle cingulate gyrus (BA 32). In the right hemisphere a separated cluster encompassed the post- and precentral gyri (BA 3/6). Furthermore, a cluster in the right MFG (BA 46) also showed significantly greater unmasked than masked priming. The inverted interaction contrast testing for significantly greater neural priming effects of masked than unmasked priming did not reveal any significant clusters.

DISCUSSION

In the present fMRI study, we investigated the neural correlates of masked and unmasked semantic priming and

Table 2. Brain Regions Demonstrating Greater Unmasked than Masked Semantic Priming

	Region	BA	Number of Voxels	Peak Voxel			
				x	y	z	z Score
L	STG	41	1233	-46	-42	16	4.13
L	STG	22		-50	-14	-2	3.80
L	STG	22		-54	-2	-8	3.62
R	STG	42	1907	52	-42	22	3.79
R	STG	22		60	-24	6	4.14
R	STG	22		62	-14	-2	3.75
R	Putamen	-		30	-12	-4	3.88
R	Hippocampus	-		32	-12	-20	3.67
R	Insula	13		42	-2	8	3.51
L	Precuneus	5	4650	-10	-60	56	4.16
L	SPL	7		-16	-62	50	3.93
L	Postcentral gyrus	3		-30	-34	58	4.19
L	Supramarginal gyrus	40		-52	-28	20	3.33
L	Precentral gyrus	6		-38	-8	48	4.27
L	SMA proper	6		-6	-8	58	4.56
L	Middle cingulate gyrus	32		-12	12	36	3.92
R	SPL	7		20	-60	56	3.81
R	Precuneus	5		4	-44	50	3.40
R	SMA proper	6		10	-2	50	3.74
R	Postcentral gyrus	3	1079	32	-30	54	4.68
R	Precentral gyrus	6		28	-22	64	4.50
R	Precentral gyrus	6		50	-8	46	3.50
R	MFG	46	452	36	36	34	3.95

The z scores were converted from t values by SPM8.

tested on concordance and difference between both conditions in a sample of 24 participants. In particular, we were interested to distinguish between brain regions that show priming effects under both subliminal and visible priming conditions and presumably support automatic priming processes and brain regions that exhibit priming effects only in the visible condition, most likely contributing to strategic priming processes.

Testing on prime visibility clearly indicated that masked primes were not consciously perceived and our manipulation was successful in probing automatic semantic processing in this priming condition. At the behavioral level, both priming conditions showed reliable priming effects, although effects were smaller in the masked than in the unmasked condition, thereby replicating previous findings (Kiefer, 2002; Kiefer & Spitzer, 2000). At the neural level, we found brain areas that were associated with semantic priming under both the masked and unmasked prime conditions, as well as brain regions exhibiting significantly greater priming under unmasked than masked conditions. However, no brain region demonstrated greater priming in the masked than in the unmasked condition suggesting that unconscious semantic processing does not involve specific pathways.

Brain Regions Associated with Both Masked and Unmasked Semantic Priming

In line with previous electrophysiological studies demonstrating masked and unmasked ERP priming effects with a similar topography (Kiefer, 2002; Kiefer & Spitzer, 2000), we found conjoint neural priming effects in both masking conditions in several brain areas. Irrespective of the masking condition, greater activation for unrelated than related trials was observed in the left FFG, pMTG, pIFG, pre-SMA, anterior insula, thalami, and anterior putamen.

Priming effects in posterior brain regions (FFG, pMTG) matched with our initial expectation to reflect automatic processing of semantic features (Kiefer & Barsalou, 2013; Kiefer & Pulvermüller, 2012; Martin, 2007; Barsalou et al., 2003; Martin & Chao, 2001). Our findings are in good accordance with results and interpretations from previous studies (Gold, Andersen, Jicha, & Smith, 2009; Gold et al., 2006; Wheatley et al., 2005) also reporting semantic priming effects in the left FFG at locations either identical or next to the locations of this study.

By contrast, involvement of the more frontal regions (pIFG, pre-SMA, and anterior insula) was not predicted. Since controlled cognitive processes such as expectancy generation or semantic matching are unlikely when the prime is masked, other processes that are differentially modulated in the presence of related and unrelated trials might have contributed to involvement of these brain areas, which, however, may relate to the LDT per se.

Activation of the left pIFG has been reported in studies on language production (for review by Price, 2000), phonological processing (McDermott, Petersen, Watson, &

Ojemann, 2003; Badre & Wagner, 2002; Fiez, 1997), and subvocal rehearsal (Rogalsky, Matchin, & Hickok, 2008; Smith & Jonides, 1999; Awh et al., 1996; Paulesu, Frith, & Frackowiak, 1993). Since LDT may involve phonological judgment to arrive at lexical decisions between words and pseudowords (Price et al., 1994), the frequently observed pIFG engagement in previous lexical decision studies (e.g., Fiebach, Ricker, Friederici, & Jacobs, 2007; Fiebach, Friederici, Müller, & von Cramon, 2002; Kiehl et al., 1999; Rumsey et al., 1997) suggests that phonological processing is automatically triggered by this specific task set (but see Heim, Eickhoff, Ischebeck, Supp, & Amunts, 2007). In that sense, differential pIFG activity for R and U trials might have emerged because the phonological decision process could be aborted earlier in the case of R trials because of the facilitated construction of the target's meaning (in the FFG), thereby resulting in lower pIFG activity. As alternative explanation it should be added, however, that even subliminal information may trigger considerable semantic conflict (see Van Opstal, Calderon, Gevers, & Verguts, 2011; for a review, see Desender & Van den Bussche, 2012). From this perspective, different degrees of relatedness between prime and target might have differentially engaged the pIFG to unconsciously select the relevant meaning of the target and to suppress the irrelevant concept of the prime (Cardillo, Aydelott, Matthews, & Devlin, 2004; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997). Finally, given its role in episodic memory encoding, differential pIFG activity might have reflected unconscious formation of episodic memory resources as suggested by episodic accounts of priming (Bodner & Masson, 2003), although independent evidence for this interpretation is lacking so far. It should be noted, however, that this study was not specifically designed to decide between these alternative interpretations of pIFG activity during semantic priming tasks.

Facilitation of phonological processing might also have driven differential activation in the anterior insula, given that the anterior insula, similar to the pIFG, has been implicated in the production and perception of language (Price, 2000; Fiez & Petersen, 1998) in general and phonological processing (Rumsey et al., 1997) and verbal working memory (Awh et al., 1996; Fiez et al., 1996) in particular. Activation of the pre-SMA has previously been reported to associate with response selection (Tremblay & Gracco, 2010; Wheatley et al., 2005; Sakai et al., 2000; Deiber, Ibanez, Sadato, & Hallett, 1996; Picard & Strick, 1996). Its differential activation upon R and U trials suggests that the effort to select the correct motor response upon words and pseudowords was again possibly lower also for related than for unrelated targets. Because the anterior putamen was activated in neuroimaging studies of motor control (Jankowski, Scheef, Huppe, & Boecker, 2009; Aron & Poldrack, 2006; Gerardin et al., 2004) and given previous evidence of anatomical (Lehericy et al., 2004; Inase, Tokuno, Nambu, Akazawa, & Takada, 1999) and functional connectivity (Wolbers et al., 2006) between

the pre-SMA and the anterior putamen, its differential involvement during R and U trials may reflect coactivation in the same way.

Brain Regions Showing Greater Unmasked than Masked Priming

Compared with the masked priming condition, the bilateral STG, SMA proper, precentral gyri, and SPLs demonstrated significantly higher priming-associated neural activation in the unmasked condition. In these regions, estimates of neural activation (see Figure 3) indicate that the significant masking by relatedness interaction was almost exclusively driven by a relatively strong increase of neural activation upon processing U trials in the unmasked condition. Activation upon R and U trials in the masked condition was equivalent in these brain regions. In the following, we argue that the associated increase in unmasked neural priming can be best interpreted in light of strategic prime processing, most likely semantic matching.

One strategic mechanism is expectancy generation (Neely et al., 1989; Posner & Snyder, 1975). Of note, however, this strategy is thought to require a prime target SOA of at least 500 msec (Chwilla et al., 1998). Because a much shorter SOA of 200 msec was used in the unmasked condition in this study, it is unlikely that expectancy generation played a role.

Most likely, within the context of the present paradigm, conscious access to the meanings of the prime and the target may have motivated participants to actively apply a semantic matching strategy (Neely et al., 1989; Lupker, 1984; Neely, 1977), which has been reported to operate even at rather short SOAs (Koivisto, 1998). Given that the prime is always a real word, a semantic relation between prime and target is set up and participants are biased to conclude that the target must also be a real word, thus facilitating the lexical decision upon R targets. However, when the meanings of the prime and the target are unrelated, the lexical decision is biased toward a nonword response, which has to be overcome to give the correct response (Neely et al., 1989).

Hence, at the neural level, semantic matching should entail different magnitudes of brain activation during related and unrelated trials. Still, there is an ongoing debate about which trials, R or U, produce greater neural activity. It was argued that a positive match in case of R trials represents a unique neural event that is associated with higher activation (Copland, de Zubicaray, McMahon, & Eastburn, 2007; Raposo et al., 2006; Henson, 2003). Alternatively and taking up the idea described by Neely et al. (1989), brain activation might increase during unrelated in comparison with related trials. First, when the meanings of the prime and the target are unrelated, it should be more difficult to bring them together, resulting in longer RTs, probably because of prolonged and deeper target processing at the neural level. Second, the nonword bias associated with unrelated target words has to be overcome, which probably

requires attentional control to resolve the occurring response conflict.

Support for the latter view, which implies higher brain activation during U trials, comes from a study conducted by Ruff, Blumstein, Myers, and Hutchison (2008). Using an explicit relatedness judgment task, neural activity was greater for unrelated than for related word pairs in the bilateral STG and left IFG. The posterior STG has also been shown to exhibit greater effects of unmasked semantic priming when the prime target SOA is long (1000 msec) than when it is short (200 msec; Rossell, Price, & Nobre, 2003). It has therefore been suggested that posterior STG plays a role in strategic processing, although its specific function remains open (Rossell et al., 2003). One possibility is that parts of posterior STG serve as semantic convergence zone, which supports semantic selection during semantic interference resolution (de Zubicaray, Wilson, McMahon, & Muthiah, 2001). Alternatively, it has been proposed that STG activity reflects activation of semantic representations (Ruff et al., 2008; Jung-Beeman, 2005). We do not generally argue against the STG as representing semantic knowledge, and our group has already shown that a posterior STG portion most likely represents acoustic features pertaining to semantic concepts (Trumpp, Kliese, Hoenig, Haarmeier, & Kiefer, 2013; Kiefer et al., 2012; Kiefer, Sim, Herrnberger, Grothe, & Hoenig, 2008). In this study, however, priming in the STG was highly specific to the unmasked condition and involved almost the entire anterior–posterior extent of the STG, rendering a semantic representation hypothesis less likely.

Holding that the STG plays a role in strategic processing, it is conceivable that the STG, together with the SMA proper, the precentral gyrus, and the SPL may have served resolving the conflict to overcome the nonword bias during semantic matching. On the one hand, conflict resolution might have occurred at the motor level because participants had to withstand pressing the wrong button. In line with that view, the SMA proper and the precentral gyrus have been implicated in conflict resolution at the motor level (Zurawska Vel Grajewska, Sim, Hoenig, Herrnberger, & Kiefer, 2011; Sumner et al., 2007). On the other hand, conflict resolution might also have taken place at the semantic level, possibly performed by the SPL, given its role in allocating spatial and non-spatial attentional resources (Bartolomeo, Thiebaut de Schotten, & Chica, 2012; Grandjean et al., 2012; Shomstein, 2012; Shomstein, Kravitz, & Behrmann, 2012; Corbetta & Shulman, 2002; Hopfinger, Buonocore, & Mangun, 2000; Nobre et al., 1997; Corbetta, Miezin, Shulman, & Petersen, 1993). It is assumed that posterior parietal areas such as the SPL receive signals for attentional adjustment from the PFC and then exert appropriate attentional control over task-relevant sensory brain regions (Shomstein et al., 2012). Although top–down attentional control has most often been demonstrated for spatial locations and visual object features, it is conceivable that the same

mechanism also applies to semantic information (Kiefer, 2007). Indeed, such evidence was provided by Hoenig and Scheef (2009), who observed posterior parietal activation during resolution of semantic ambiguity. Turning to the present findings, the SPL might have aided in overcoming the nonword bias associated with U trials by directing more attention to the meaning of the target (Neely et al., 1989). In support of that notion, a role of the SPL in “implementing strategic adjustments in top–down control” in the context of conflict processing has also been suggested by Grandjean et al. (2012, p. 8) to explain their finding of greater SPL activity for incongruent than for congruent trials in a modified Stroop task (Stroop, 1935).

Conclusions

Using a within-subject design in a sample of 24 participants, we determined commonalities and differences in semantic priming effects in the presence of masked and unmasked primes at the behavioral and neural level. Both conditions revealed the typical behavioral priming effect with shorter RTs for semantically related than unrelated word pairs, obtained within a LDT. In accordance with our expectation, conjoint neural priming under both masking conditions was observed in the FFG, most likely reflecting automatic pre-activation of semantic features. Conjoint activation of the pIFG and pre-SMA may have been driven by unconscious selection of relevant meaning during the LDT that occurs under both unconscious and conscious viewing conditions. When primes were not masked and therefore consciously accessible, brain regions located in the frontal, temporal, and parietal lobes showed significantly higher activation upon unrelated than related trials, most likely driven by semantic matching and subsequent interference resolution as the mechanisms of action. However, masked priming did not elicit greater activity than unmasked priming in any brain region. Hence, unconscious and conscious semantic priming activates a common set of brain areas, in which semantic processing presumably occurs in an automatic fashion. However, distinct neural activity in the unmasked condition suggests that prime awareness gives rise to additional, presumably strategic processes. The present results therefore indicate that masked and unmasked semantic priming partially depend on dissociable mechanisms at the neural and most likely also at the functional level.

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