Unconscious Word Processing Engages a Distributed Network of Brain Regions

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Abstract

■ A briefly exposed visual stimulus may not be consciously perceived if it is preceded and followed by a dissimilar visual pattern or mask. Despite the subject's lack of awareness, prior behavioral studies have shown that such masked stimuli, nevertheless, engage domain-specific processes [Dehaene, S., Naccache, L., Cohen, L., Le Bihan, D., Mangin, J.-F., Poline, J.-B., et al. Cerebral mechanisms of word masking and unconscious repetition priming. *Nature Neuroscience, 4,* 752–758, 2001; Bar, M., & Biederman, I. Subliminal visual priming. *Psychological Science, 9,* 464–469, 1998; Dehaene, S., Naccache, L., Le Clec'H, G., Koechlin, E., Mueller, M., Dehaene-Lambertz, G., et al. Imaging unconscious semantic priming. *Nature, 395,* 597–600, 1998; Whalen, P. J., Rauch, S. L., Etcoff, N. L., McInerney, S. C., Lee, M. B., & Jenike, M. A. Masked presentations of emotional facial expressions modulate amygdala activity without explicit knowledge. *Journal of Neuroscience, 18,* 411–418, 1998; Marcel, A. J. Conscious and unconscious perception: Experiments on visual masking and word recognition. *Cognitive Psychology, 15,* 197–237, 1983]. Masking thus provides a method for identifying language processes that are preattentive and automatic. Functional magnetic resonance imaging used in concert with masking may identify brain regions engaged by these unconscious language processes. In an adaptation design, subjects viewed a continuous stream of masked words and masked nonwords while performing an unrelated detection task, in which they were asked to make a response to a visible colored nonword stimulus (i.e., ampersands in red or blue font). Most trials were masked nonwords and masked words were presented once every 12–15 sec. The task ensured participant engagement, while the masked nonword baseline controlled for perceptual and orthographic processing. Participants were naïve to the purpose of the experiment and testing indicated that they did not consciously perceive either the words or nonwords. Masked words, but not masked nonwords, strongly activated left hemisphere language regions, including Broca's area, the angular gyrus, and the lateral temporal lobe. Differential activation of the posterior corpus callosum was also observed. ■

INTRODUCTION

Brain lesion and imaging studies have established that visual word processing engages a distributed network of primarily left hemisphere brain regions (Damasio, Grabowski, Tranel, Hichwa, & Damasio, 1996; Mesulam, 1990) including regions of the temporal, parietal, and inferior frontal cortex (Binder et al., 1997; Davis & Wada, 1978). Neuroimaging can contribute to the functional analysis of this distributed system by determining whether putative stages of word analysis, such as lexical access, have distinct anatomical loci. This analysis is complicated, however, by the coactivation of cognitive processes unrelated to word processing per se—either explicitly through task demands or implicitly through the engagement of strategic processes. These extraneous cognitive processes likely influence the pattern of activation obtained in even the simplest word processing tasks. It is perhaps for this reason that in many studies, visually presented words evoke widespread and bilateral brain activity including regions previously associated with decision-making, working memory, and other executive processes (Binder et al., 1997).

Through the use of short stimulus durations and masking procedures, stimuli can be presented that are not consciously perceived by the subject (Bar & Biederman, 1998; Whalen et al., 1998). Masked words are presumed not to engage strategic and task-related processes, and thus, have the potential to simplify functional analysis. However, numerous behavioral studies have demonstrated that masked words speed the recognition of subsequent visible semantically related words, and thus, activation evoked by masked words should encompass brain regions involved in the automatic activation of a word's semantic representation.

Dehaene et al. (1998, 2001) used functional magnetic resonance imaging (fMRI) to search for brain activity evoked by masked words. They observed that masked words evoked discrete foci of activity in the left fusiform gyrus and left precentral gyrus when compared to masked intervals of the same duration in which no stimulus was present (i.e., blank intervals). This pioneering study was first to establish the important fact that fMRI has sufficient sensitivity to measure brain activity

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evoked by masked stimuli; however, we found two aspects of the results surprising. First, no activation by masked words was observed in brain regions known to support reading, such as the left angular gyrus, nor was activation observed in other language areas such as the left posterior frontal lobe and left posterior temporal regions. The absence of activation in these and other regions was suggested to underlie the subjects' lack of awareness for these stimuli (Dehaene et al., 2001), and thus, these regions may provide the neural substrate for conscious awareness.

However, as prior behavioral studies have established that masked words can prime subsequent semantically related visible words, masked words must be processed to a high level (Greenwald, Draine, & Abrams, 1996; Cheesman & Merikle, 1984; Balota, 1983; Marcel, 1983; Fowler, Wolford, Slade, & Tassinary, 1981). Electrophysiological studies have examined the influence of masked words upon the N400 component of the event-related potential (ERP) (Kiefer, 2002; Stenberg, Lindgren, Johansson, Olsson, & Rosen, 2000; Brown & Hagoort, 1993). N400 is evoked by words that have semantic meaning and is diminished when the evoking word has been primed by identity, by a semantically related word, or by the context of a sentence (Bentin, McCarthy, & Wood, 1985; Rugg, 1985; Kutas & Hillyard, 1984). It has been demonstrated that the N400 component evoked by visible words was diminished in amplitude when preceded by semantically related masked words (Kiefer & Brendel, 2006; Kiefer, 2002; Deacon, Hewitt, Yang, & Nagata, 2000; Kiefer & Spitzer, 2000). Moreover a study by Stenberg et al. (2000) suggests that masked words themselves may evoke ERPs that are influenced by semantic priming. In their study, subjects were given a semantic category (such as "furniture") and then showed a series of words of varying short durations that were followed by a mask. Some of the masked words were visible and some were not. Stenberg et al. showed that masked words that were not visible, nevertheless, evoked ERPs that differed in amplitude depending upon whether the masked words were related or unrelated to the semantic category. These differential semantic priming ERP effects occurred at a latency of about 400 msec after the onset of the masked words. However, others have failed to find an effect of the presentation of masked primes on N400 amplitude (Brown & Hagoort, 1993). Recently, Holcomb, Reder, Misra, and Grainger (2005) have reported a correlation between N400 amplitude and masked prime visibility in a semantic priming paradigm. Thus, the influence of masked words on the N400 remains a controversial topic.

Recently, Cohen et al. (2000, 2002) have labeled a region in the left fusiform gyrus the visual word form area, and suggested that this region is sensitive to the visual presentation of word forms. Several findings support this conceptualization of the region, including greater activation to words than pseudowords (Fiebach, Friederici, Muller, & von Cramon, 2002), evidence of an electrophysiological component sensitive to semantic processing, the recognition potential, which is localized to the inferior occipito-temporal cortex (Martin-Loeches, Hinojosa, Gomez-Jarabo, & Rubia, 2001), and sensitivity to word frequency (Assadollahi & Pulvermuller, 2003). However, others have found activation in this region to a variety of other tasks, such as auditory word presentation, naming colors and words, and thus, have suggested that this region may not be specialized to visual language processes (Price & Devlin, 2003).

Subdural electrophysiological recordings from the fusiform gyrus made by our group have demonstrated selective responses to letterstrings when compared to objects, faces, or scrambled stimuli, but not differentiation between word and nonword letterstrings (McCarthy, Nobre, Bentin, & Spencer, 1995; Nobre & McCarthy, 1995; Nobre, Allison, & McCarthy, 1994). Polk and Farah (1998) found greater activation in this region for individually presented letters versus digits, suggesting that words per se are not required to elicit activation in this region. These results implicate the fusiform in letter level, but not lexical or semantic processes, and suggests that the fMRI activation observed by Dehaene and colleagues may be related to the presence of letters rather than words.

To date, no study has compared masked words and masked nonwords to address this potential confound (i.e., whether brain regions sensitive to masked stimuli responded on the basis of letters rather than words). We examined the neural basis of automatic and unconscious word processing by conducting a neuroimaging study that compared fMRI activation evoked by masked words and masked nonwords (Figure 1B). In this adaptation design, the continual presentation of masked nonwords served to maximally engage areas that responded only to perceptual or orthographic properties of the stimuli (Grill-Spector & Malach, 2001). Within this context, any brain region that demonstrated activation above baseline must have responded on the basis of properties other than perceptual and orthographic (e.g., lexical properties, semantic content). Participants also performed a color detection task that was unrelated to the presentation of masked words and nonwords. Prior to imaging, we conducted a behavioral study to confirm that masked words are processed to the semantic level (Figure 1A).

METHODS

Subjects

Fourteen subjects (ages 20–34 years, mean 23.1 years, 7 men) participated in the preliminary behavioral lexical decision task (LDT). A different group of 12 subjects (ages 18–26 years, mean 22.3 years, 3 men) participated in the main fMRI experiment. All participants were right-handed, native English-speaking healthy young adults

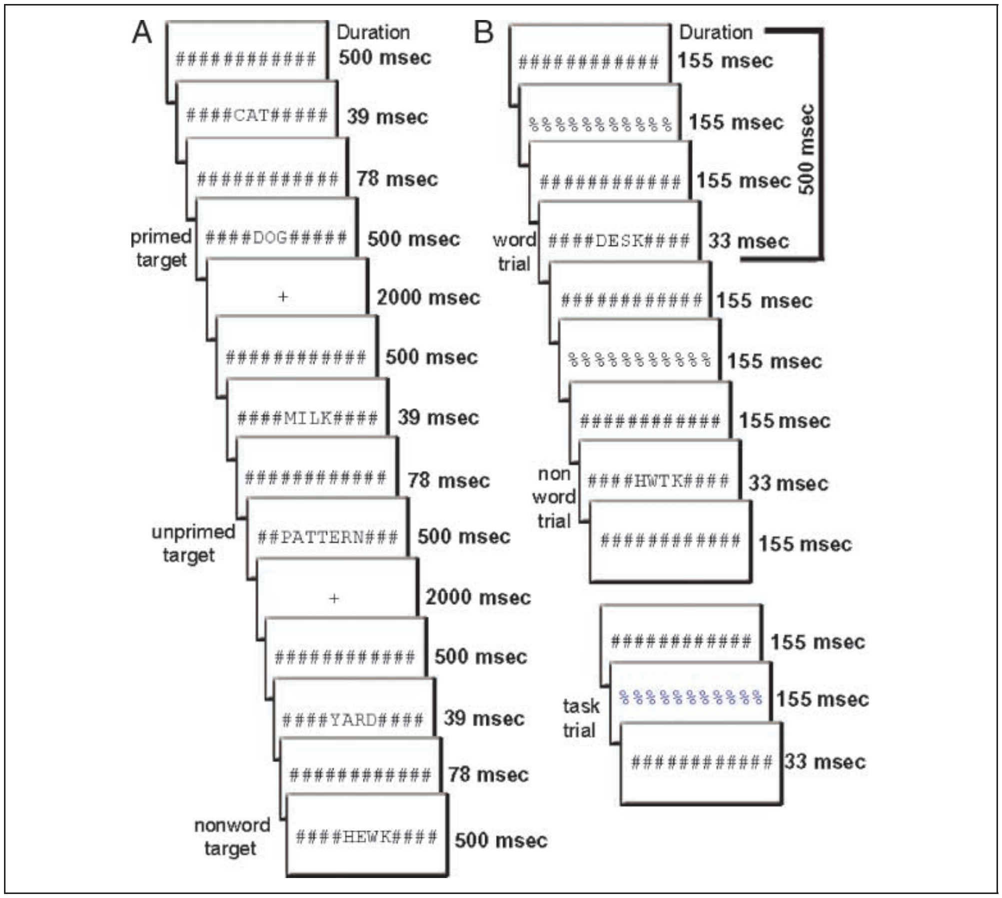

Figure 1. Experimental design. (A) In the lexical decision task, masked primes were followed by a visible word (semantically related or unrelated) or a visible pronounceable nonword to which participants made lexical decisions. (B) In the event-related fMRI experiment, the sequence for a critical trial consisted of alternating pound signs and percent signs, in between which a word or nonword (trial duration = 500 msec) was inserted. Incidental to the critical stimuli, visible colored stimuli were displayed to which participants made a button press.

who provided informed consent and were paid for their participation. All experimental procedures were approved by Duke University's Institutional Review Board.

Materials and Procedure

In the LDT, subjects decided whether visible letter-strings were words or nonwords. A masked word preceded each visible letterstring, which could be a word, semantically related (n = 50) or unrelated (n = 50) to the prime, or a pronounceable nonword (n = 100; Figure 1A). All stimuli were matched for length. The average lengths for the stimulus categories were as follows: related word prime, 4.92; related word target, 4.83; unrelated word prime, 4.80; unrelated word target, 4.74; word prime (for pseudoword target), 4.70; pseudoword target, 4.80. Words were matched for frequency. The average frequencies for the stimulus categories were as follows: related word prime, 70.9; related word target, 81.1; unrelated word prime, 73.3; unrelated word target, 74.7; word prime (for pseudoword target), 76.3; pseudoword target, n/a. During the LDT, the display refreshed at 75 Hz, or approximately every 13 msec. All stimuli onsets were time-locked to a screen refresh cycle.

In the event-related fMRI experiment, critical stimuli consisted of words and nonword letterstrings that were masked and displayed in a fixed width font. Words were concrete nouns (average length = 4.82; average frequency = 56.45; average imageability = 596.6). Nonwords were created by randomly selecting consonants to form consonant strings (average length = 4.82). Word and nonword stimuli were not repeated. Each word and nonword stimulus was padded on either side with pound signs so that letters were centered and each stimulus was 12 characters in length. This ensured that the same amount of the visual field was occupied at any given time during the experiment. Word and nonword trials occurred at the end of a sequence of four successive stimuli, each 12 characters in length (Figure 1B).

Participants viewed a constantly changing visual display in which a critical stimulus occurred every 500 msec. Most trials were masked nonwords (n = 5380), and masked words (n = 200) were presented once every 12–15 sec. All word and nonword strings were preceded and followed by longer duration pound sign strings, which served as effective pattern masks. The pound sign strings, in turn, alternated with percent sign strings such that the subject experienced a continuously changing visual stream that flipped between pound and percent signs. During the fMRI experiment, the display refreshed at 60 Hz, or approximately every 16 msec. All stimuli onsets were time-locked to a screen refresh cycle.

The masked nonword baseline ensured that brain regions responsive to physical features and orthography would be continuously active (Grill-Spector & Malach, 2001). Any brain region whose activation evoked by masked words exceeds this baseline must be engaged in a higher level of processing (e.g., lexical or semantic). Subjects were instructed to make a choice button press response when they detected a pound sign string presented in either blue or red font. The purpose of the task was to keep subjects engaged during the scan. These target events occurred infrequently (interval = 9–82.5 sec, mean = 25 sec) and, critically, were not in close temporal proximity to the masked word trials.

The subjects were never informed that words or nonwords would be presented. In order to evaluate subjects' perceptions of the masked stimuli, both subjective and objective assessments were conducted. Prior to neuroimaging, participants were shown individual masked trials and were asked to report "anything and everything that you see." After the imaging experiment, subjects were verbally questioned about what they experienced and performed a forced-choice experiment in which new masked word trials were presented, and the subjects were asked to choose which word had just been displayed from two clearly visible alternatives. All stimuli were displayed on LCD goggles using the CIGAL experimental control program (Voyvodic, 1999).

Functional Magnetic Resonance Imaging

Functional images, sensitive to blood oxygenation-level-dependent (BOLD) contrast, were acquired using an inverse spiral pulse sequence (TR = 1.5 sec; TE = 35 msec; FOV = 24 cm; image matrix = 64^2; 34 contiguous axial slices; voxel size = 3.75 × 3.75 × 3.8 mm) on a GE 4.0-Tesla LX NVi MRI scanner.

Each of 10 runs consisted of the acquisition of a time series of 198 brain volumes. Four initial radio-frequency excitations were performed to achieve steady-state equilibrium. High-resolution structural images were acquired using a 3-D fast SPGR pulse sequence (TR = 12.2 msec; TE = 5.3 msec; FOV = 24 cm; image matrix = 256^2; voxel size = 0.9375 × 0.9375 × 1.9 mm). A semiautomated high-order shimming program was used to ensure global field homogeneity.

Data Analysis

Preprocessing was performed using SPM99 software (Welcome Department of Cognitive Neurology, London, UK). Images were corrected for slice order acquisition and head motion, normalized to a standard MNI stereotaxic space (Montreal Neurological Institute, Montreal, Canada), and smoothed (FWHM = 8 mm). Short epochs consisting of the image volumes time-locked to critical stimuli were extracted from the continuous time series of volumes and averaged into word and nonword bins. Because nonword trials were more numerous than word trials, a straight comparison of word trials to nonword trials would be unbalanced. Therefore, we generated several random samples of nonword trials. Each sample was equal in number to the number of word trials (n = 200). No statistical differences among these nonword samples were found. We then took the average of three random samples of nonword trials for use in the comparison between the critical condition and nonword trials.

Active voxels were identified as those that were found to be significant in both fixed and random effects analyses. In the fixed effects analysis, active voxels were determined for each subject by regressing an empirically derived hemodynamic template with the averaged time courses for word and nonword trials. Active voxels were identified as those for which the correlation of the template and the voxel's average time course was significant at $p < .001$. In the random effects analysis, the significance of the correlation for each voxel across the 12 subjects was calculated ($p < .05$). The average t map for 12 subjects and the results of the random effects analysis are presented on a brain normalized to MNI space.

RESULTS

Behavioral Performance

In the LDT, the masked primes speeded reaction times to semantically related words compared to semantically unrelated words [facilitation = 9 msec; $F(1, 13) = 6.07$, $p = .028$; average reaction time to related targets = 651 msec; unrelated targets = 660 msec]. The subjects' average accuracy in the colored trial detection task was 84.61% (SD = 12.62%) and the average reaction time was 797.11 msec (SD = 140.11 msec).

Functional MRI

Using the methods described, we searched for voxels in which masked words evoked a larger hemodynamic response than masked nonwords. A random effects statistical analysis revealed areas in the left hemisphere that specifically responded to the masked words but not to the masked nonwords ($p < .001$), including the inferior frontal gyrus (158 voxels; MNI: −58, 27, 10), the angular gyrus (423 voxels; MNI: −46, −73, 33), and the inferior temporal gyrus (54 voxels; MNI: −56, −57, −11), which extended to the middle temporal gyrus (Figure 2A). At these loci, the masked words evoked a robust hemodynamic response, whereas the masked nonwords evoked no measurable response (Figure 2B).

We also observed differential activation within the white matter tracts that constitute the splenium of the corpus callosum (18 voxels; MNI: −3, −36, 14; Figure 3). In order to confirm that this activation originated in the white matter and was not an artifact of smoothing or misregistration during normalization, we conducted additional

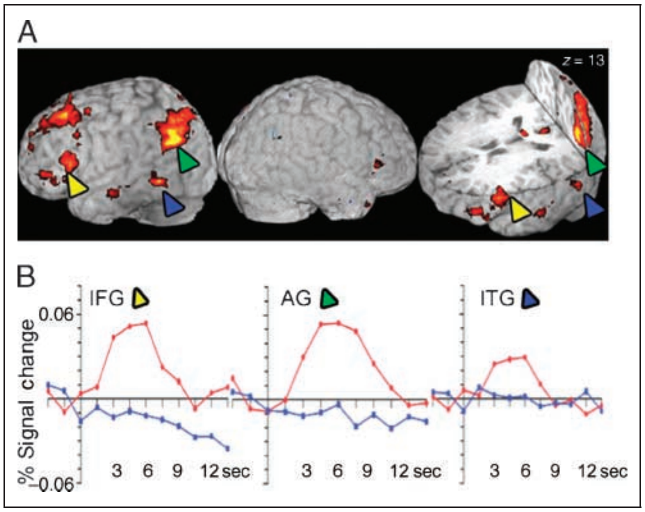

Figure 2. Areas of activation that differentiated masked words from masked nonwords. (A) Activations ($p < .001$) were present in the left inferior frontal gyrus (yellow triangle; MNI: −58, 27, 10), the angular gyrus (green triangle; MNI: −46, −73, 33), and the inferior temporal gyrus (blue triangle; MNI: −56, −57, −11); red represents areas that significantly responded to masked words but not masked nonwords in both fixed and random effects analyses. Results are overlaid on a single subject's normalized brain. (B) Hemodynamic time courses represent the average time course (−3 sec to 13.5 sec) for regions found to significantly respond to masked words in both fixed and random effects analyses. Red lines indicate the response to masked words, blue lines indicate the response to masked nonwords.

anatomically based region-of-interest (ROI) analyses. Individual ROIs were drawn in the splenium of the corpus callosum in each subject's own anatomy. Analysis confirmed that masked words elicited a greater response than masked nonwords. A second ROI analysis was conducted to confirm that activation in the splenium was not attributable to spatial smearing from the nearby gray matter. This analysis demonstrated that there was no significant hemodynamic response to either masked words or nonwords in the gray matter closest to the splenium (Figure 3C).

Other areas significant only in fixed effects analyses include the left superior frontal and posterior cingulate. Masked nonwords did not elicit significant activation in any of the brain regions that were significantly activated by masked words.

Visibility Measures

Subjective measures of masked word visibility were acquired before and after acquisition of functional images. At no time did any participant report seeing letters, words, or nonwords. In the forced-choice detection task, subjects did not perform statistically different from chance [$t(11) = -0.95, p = .364$], confirming that our masking procedure was successful.

DISCUSSION

In the present experiment, we sought to directly compare brain activation evoked by masked words and masked nonwords. Objective and subjective measures confirmed that participants were naive to the experimental manipulation and did not consciously perceive nonwords, words, or their constituent letters. Nevertheless, we found that masked words, but not masked nonwords, elicited significant activation in expected language regions of the left hemisphere, including the inferior frontal gyrus, the angular gyrus, and posterior regions of the lateral temporal cortex.

Damage to the left inferior frontal gyrus can result in Broca's aphasia (Broca, 1861). Recent functional imaging studies with visible words have implicated this region

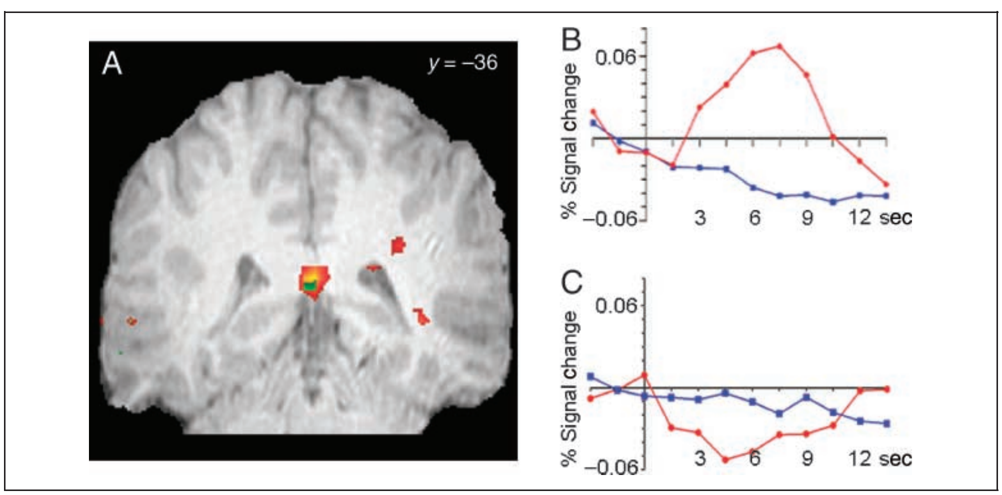

Figure 3. White matter activations. (A) Differential activation was present in the splenium of the corpus callosum (MNI: −3, −36, 14). Red represents areas that significantly responded to masked words but not masked nonwords in a fixed effects analysis, green represents areas that significantly responded to masked words but not masked nonwords in both fixed and random effects analyses. Results are overlaid on a single subject's normalized brain. (B) Hemodynamic time courses for the splenium. Red lines indicate response to masked words, blue lines indicate the response to masked nonwords. (C) Hemodynamic responses from gray matter regions closest to the corpus callosum. Red lines indicate response to masked words, blue lines indicate the response to masked nonwords.

in the syntactic and semantic aspects of language comprehension and semantic aspects of working memory (Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997; Petersen, Fox, Posner, Mintum, & Raichle, 1988). The angular gyrus, particularly in the left hemisphere, has been implicated in reading (Rumsey et al., 1999; Horwitz, Rumsey, & Donohue, 1998). Damage to this structure, or the white matter tracts connecting it with the visual cortex, can produce alexia (Dejerine, 1891). The functional connectivity of the angular gyrus is correlated with reading ability, and functional disconnection in this area has been linked to dyslexia (Rumsey et al., 1999; Horwitz et al., 1998; Dejerine, 1891). Lesions of the temporal lobes cause impairments in semantic processes, such as naming, that are consistent with deficits in semantic knowledge stores (Hodges, Patterson, Oxbury, & Funnell, 1992). Numerous functional imaging studies have reported activation in temporal regions during tasks that involve semantic processes (for a review, see Price, 1998).

Additionally, we observed differential activation in the splenium of the corpus callosum. Follow-up analyses limited the possibility that this activation was due to artifacts of acquisition or postprocessing. The splenium is a major communicative fiber tract between the cerebral hemispheres. If surgically severed, patients cannot read words presented to the right hemisphere (Sidtis, Volpe, Holtzman, Wilson, & Gazzaniga, 1981). Damage to this area can also cause alexia (Ajax, Schenkenberg, & Kosteljanetz, 1977). Although white matter activations are not typically reported in fMRI studies, the BOLD signal is sensitive to changes in blood oxygenation levels and, although the white matter is less vascularized than the gray matter, it nevertheless requires oxygen. The sensitivity of high-field imaging combined with signal averaging of a large number of trials may have provided the conditions for observing such small but reliable signals. The callosal activation was maximal at the center of the splenium where the greatest spatial concentration of fibers occurs. The absence of white matter activation throughout the entire tract may be due to the spatial dispersion of fibers distal to the splenium, which may make the detection of activation less likely.

Our results provide a striking contrast to previous functional imaging experiments of masked words and conflict with speculations recently offered about the neural substrates of conscious experience. As reported here, masked words evoked distributed activity in left hemisphere brain regions well known on the basis of neurological lesions and prior imaging studies using supraliminal stimuli to be engaged in reading and language processing. It has been postulated that visual consciousness depends on projections to the frontal lobes, and frontal activation has been associated with conscious perception in blindsight patients (Dehaene, 2001; Sahraie et al., 1997; Crick & Koch, 1995). However, our results indicate that activation of at least some frontal regions is insufficient to give rise to awareness.

By presenting masked letterstrings every 500 msec, our experiment was deliberately designed to continuously activate brain regions associated with letter processing. Thus, activation evoked by the presence of letters per se should not be measurable. It is notable, therefore, that no activity that differentiated masked words and nonwords was observed in the fusiform gyrus. Although a negative finding, it is consistent with our conjecture that prior activation of this region by masked words compared to blank intervals (Dehaene et al., 2001) reflected letter-based processing. However, Dehaene and colleagues showed that activity in the fusiform evoked by a visible word was diminished if the visible word was immediately preceded by a masked version of the same word. This identity priming occurred even if the masked prime was in a different case than the visible word. On this basis, Dehaene attributed activity in the fusiform to the processing of ''specific information about word identity'' (Dehaene et al., 2001). This attribution is not supported by the present results that showed no differential activation of the fusiform to words and nonwords. Rather, we suggest that higher brain regions associated with the semantic representation of a masked word provide recurrent activation or feedback to lower perceptual regions. This hypothesis is consistent with subdural recordings from letterstring-specific regions of the fusiform gyrus, in which effects of top-down attentional manipulations are apparent at late but not early time windows (Nobre, Allison, & McCarthy, 1998).

In this experiment, we sought to test the hypothesis of whether the brain differentially responds to masked words and masked nonwords in the absence of any explicit task or linguistic demands. In this experiment, we rule out the possibility that masked words elicit activation only when presented in conjunction with visible words (i.e., the standard masked priming task). The word and nonword stimuli differed on several factors, including pronounceability, orthographic complexity, and bigram frequency. It is possible that any of these factors could be responsible for the differences in activations that were observed here. We do not believe that the differences in activation are due to orthographic factors such as the presence of vowels or differences in syllables. We have recently collected pilot data comparing masked content words to masked function words. These data suggest that the activations are not based solely on the presence of sublexical units or the presence of vowels.

Here we demonstrated activation in a distributed network of left hemisphere brain regions evoked by masked words but not masked nonwords despite the subject's lack of conscious awareness of those words. As our behavioral study showed that masked words facilitated the processing of semantically related words, those brain regions activated by masked words form the likely neural substrates for semantic representations. Among those areas activated here, prior research supports the lateral temporal cortex, and possibly the inferior frontal gyrus, as candidate brain loci for storing semantic representations. Our results are inconsistent with the notion that activity in these areas in and of itself underlies conscious perception.

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