Automatic Priming of Semantically Related Words Reduces Activity in the Fusiform Gyrus

Thalia Wheatley, Jill Weisberg, Michael S. Beauchamp, and Alex Martin

Abstract

■ We used rapid, event-related fMRI to identify the neural systems underlying object semantics. During scanning, subjects silently read rapidly presented word pairs (150 msec, SOA = 250 msec) that were either unrelated in meaning (ankle–carrot), semantically related (fork–cup), or identical (crow–crow). Activity in the left posterior region of the fusiform gyrus and left inferior frontal cortex was modulated by word-pair relationship. Semantically related pairs yielded less activity than unrelated pairs, but greater activity than identical pairs, mirroring the pattern of behavioral facilitation as measured by word reading times. These findings provide strong support for the involvement of these areas in the automatic processing of object meaning. In addition, words referring to animate objects produced greater activity in the lateral region of the fusiform gyri, right superior temporal sulcus, and medial region of the occipital lobe relative to manmade, manipulable objects, whereas words referring to manmade, manipulable objects produced greater activity in the left ventral premotor, left anterior cingulate, and bilateral parietal cortices relative to animate objects. These findings are consistent with the dissociation between these areas based on sensory- and motor-related object properties, providing further evidence that conceptual object knowledge is housed, in part, in the same neural systems that subserve perception and action. ■

INTRODUCTION

Early research on category-specific disorder patients led Warrington, Shallice, and McCarthy to posit that conceptual knowledge was neurally organized by object properties (Warrington & McCarthy, 1987; Warrington & Shallice, 1984). This property-based approach has been supported by neuropsychological investigations (e.g., Silveri, Daniele, Giustolisi, & Gainotti, 1991; Gainotti, 1990) and neuroimaging studies with normal subjects demonstrating differential activation of brain regions associated with different object properties (e.g., Thompson-Schill, Aguirre, D'Esposito, & Farah, 1999; Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995). Specifically, the lateral temporal cortex has been shown to respond to object motion, the left ventral premotor and posterior parietal cortex to motor tasks requiring manipulation, and the ventral temporal cortex, centered on the fusiform gyri, to visual properties of objects such as form and color. Most importantly, these areas are also active during tasks requiring access to semantic knowledge of items underpinned by these properties (see Thompson-Schill, 2003; Bookheimer, 2002; Martin & Chao, 2001, for reviews). The lateral temporal cortex responds not only to veridical motion, but to static pictures of implied motion (e.g., a cup in mid-fall or an athlete mid-run; Kourtzi & Kanwisher, 2000; Senior et al., 2000), semantic judgments about actions depicted in static pictures (Kable, Lease-Spellmeyer, & Chatterjee, 2002), and the generation of action words in response to both object pictures and their written names (e.g., Martin, Haxby, et al., 1995). Left ventral premotor and posterior parietal cortices respond to viewing and naming of common tools (e.g., Chao & Martin, 2000; Grafton, Fadiga, & Arbib, 1997; Martin, Wiggs, Ungerleider, & Haxby, 1996) and imagined hand movements (Naito et al., 2002; Gerardin et al., 2000; Decety et al., 1994), suggesting that these areas store the functional knowledge of the types of actions afforded by those objects. Similarly, the ventral temporal cortex, centered on the fusiform gyri, is active during retrieval of form and color information (color word generation: Chao & Martin, 1999; Wiggs, Weisberg, & Martin, 1999; Martin et al., 1995; property verification: Thompson-Schill, Aguirre, et al., 1999). Together these findings suggest that the same systems important for perception and action also house conceptual representations of these properties. However, this suggestion is not without controversy. The posterior ventral temporal cortex, in particular, is robustly associated with the perception of object form but support for its role in object semantics remains tentative due to a number of perceptual confounds in previous studies. The motivation behind the present

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study was to provide a stringent test for whether this area is indeed driven by concepts as well as percepts.

One way to deduce the processing characteristics of a cortical region is through its adaptation dynamics. First observed in the macaque inferotemporal cortex, repetition of a visual stimulus has been associated with reduced neural firing (see Desimone, 1996, for a review). Subsequent monkey studies reported this ''repetition suppression'' under conditions that preclude controlled processing (e.g., during passive fixation: Vogels, Sary, & Orban, 1995; under anesthesia: Miller, Gochin, & Gross, 1991, and after cholinergic blockade: Miller & Desimone, 1993), suggesting that this suppression reflects an automatic tuning of the neural response. Importantly, this ''repetition suppression'' also survives transformations between presentations, such as size and shape, indicating that repetition suppression is not limited to identical repetitions of a stimulus, but rather reflects more flexible, abstract representations (in monkeys: Ito, Tamura, Fujita, & Tanaka, 1995; Lueschow, Miller, & Desimone, 1994; in humans: Dehaene, Jobert, et al., 2004; Grill-Spector et al., 1999). Several authors have suggested that this neuronal suppression reflects more efficient processing and may be linked to similar repetition-related reductions in blood flow observed in neuroimaging studies (see Henson, 2003; Schacter & Buckner, 1998; Wiggs & Martin, 1998, for reviews).

A recent study suggests that this suppression effect is not only observed with perceptual repetitions, but may similarly track conceptual repetitions. Koutstaal et al. (2001) found hemodynamic decreases in the ventral temporal cortex when participants viewed different exemplars of the same object type (e.g., pictures of different umbrellas), suggesting that this area may be involved in conceptual processing (but see Vuilleumier, Henson, Driver, & Dolan, 2002). Unfortunately, however, this interpretation remains speculative as the presence of shared physical features among exemplar pictures permits a nonconceptual interpretation. The observed decreases, smaller than those seen with identical repetitions, could therefore be the effect of partial physical overlap between the pictures of two exemplars.

Such pictorial confounds can be circumvented by the use of verbal stimuli, such as the written names of objects, which overlap in meaning alone. Indeed, the observation that category-specific patients were impaired with object names as well as pictures led Warrington and Shallice (1984) to hypothesize that the underlying impairment was conceptual rather than perceptual. Numerous studies since have demonstrated that words can facilitate the semantic processing of subsequently presented related words (see Neely, 1991, for a review) and have linked this increased efficiency in semantic processing to specific neural substrates, including the ventral occipito-temporal cortex (e.g., silent reading of object names: Bookheimer, Zeffiro, Blaxton, Gaillard, & Theodore, 1995; generating color and action words to object names: Martin, Haxby, et al., 1995; semantic match-to-sample using words: Vandenberghe, Price, Wise, Josephs, & Frackowiak, 1996; property verification task: Chao, Haxby, & Martin, 1999). Still, one could argue that the words in these tasks triggered visual imagery, which then recruited the ventral occipito-temporal cortex indirectly, rather than this area doing any conceptual legwork. Indeed, fusiform gyrus activity has been associated with object imagery (Ishai, Ungerleider, & Haxby, 2000; O'Craven & Kanwisher, 2000), word imageability (Wise et al., 2000), imagery associated with property verification tasks (Kan, Barsalou, Solomon, Minor, & Thompson-Schill, 2003), and with the generation of mental images from spoken words relative to passive listening (D'Esposito et al., 1997). This area's role in object semantics, therefore, is best understood through paradigms that avoid both pictorial stimuli and tasks that require or encourage the explicit generation of mental pictures. Avoiding perceptual confounds behooves the use of nonpictorial stimuli. Confounds of visual imagery are more tricky. One approach is to present stimuli rapidly (SOA $<$ 400 msec) so that the minimum processing time needed to generate explicit imagery is not available (see Neely, 1991, for a review of automatic vs. controlled processes).

The first brain imaging studies to examine semantic processing using rapidly presented words were blocked designs using the lexical decision task (LDT), which consists of deciding if a word is a real word or not. Mummery, Shallice, and Price (1999) hypothesized that semantic overlap between primes and targets (SOA = 250 msec) should yield a decreased hemodynamic response most commonly associated with visual (object) repetitions. Using positron emission topography (PET), they found less activity in the left anterior temporal cortex when participants made lexical decisions during runs with a high proportion of related words compared to runs with a lower proportion of related words, leading to the inference that this area (but not the ventral occipito-temporal cortex) was sensitive to semantics. An fMRI study using a similar design compared primed and unprimed lexical decisions but failed to observe the same left-lateralized activity (Rossell, Bullmore, Williams, & David, 2001). However, directly contrasting the primed and unprimed LDT tasks may have masked automatic semantic effects common to both conditions. Indeed, when the authors compared LDT to a simple motor task, they observed activity in the expected semantic areas (e.g., left fusiform, left inferior frontal cortex; Rossell et al., 2001). Moreover, the blocked design itself may have obscured more automatic semantic effects by introducing controlled processes (such as expectancy effects and cognitive strategies).

More recently, neuroimaging studies have employed more sophisticated event-related lexical decision paradigms. In contrast to previous reports, these studies used an automatic semantic priming paradigm with very

short durations between the onsets of the first and second words of each pair. Although the temporal resolution of fMRI is too slow to directly observe the neural response to the second stimulus (repetition), a technique called magnetic resonance adaptation was used to estimate its amplitude. By measuring the response to the first and second stimuli together, one assumes that the response to the first stimulus is equal across conditions and that any difference in the observed response is due to differential contributions of the second stimulus. This approach has been used in several recent reports using lexical decision (Copland et al., 2003; Kotz, Cappa, von Cramon, & Friederici, 2002; Rissman, Eliassen, & Blumstein, 2003; Rossell, Price, & Nobre, 2003). However, in these studies, the use of different types of semantic associations (i.e., strong associates, weak associates, within-category pairs, and auditory and visually presented) and divergent results make interpretation difficult. Although three of the studies reported left-lateralized decreased activity (i.e., adaptation) for related compared to unrelated word pairs, each observed decreases in a different region: left anterior medial-temporal cortex (Rossell et al., 2003); left middle temporal gyrus (MTG) (Copland et al., 2003; but see Kotz, Cappa, von Cramon, & Friederici, 2002 for *increased* activity in left MTG for related pairs); and left anterior superior temporal gyrus (Rissman et al., 2003). Interestingly, however, consistent across all three studies was reduced activity in the left inferior prefrontal cortex (LIPFC) for related pairs compared to unrelated pairs (Copland et al., 2003; Kotz et al., 2002; Rissman et al., 2003), thus appearing to challenge the characterization of this area as a ''semantic executive system'' recruited only during controlled processing (whether semantic knowledge retrieval: Wagner, Pare-Blagoev, Clark, & Poldrack, 2001; Wagner, Desmond, Demb, Glover, & Gabrieli, 1997 or in response to selection demands: Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997).

The reliance on lexical decision paradigms to examine the neural correlates of semantic priming is problematic. Although the LDT magnifies reaction time differences between primed and unprimed words, its appropriateness to distinguish semantic processes within an imaging paradigm is less clear. First, the LDT requires the subject to perform a host of cognitive processes extraneous to semantic retrieval (e.g., decision-making, response selection, and adopting a mental strategy across trials), which necessarily have their own associated neural circuitry. At best, the recruitment of additional neural resources makes it difficult to distinguish more general semantic retrieval processes from those uniquely associated with the LDT; at worst, this activity may obscure more subtle semantic activity all together. Second, the semantic nature of the task is arguably weak. Nonwords typically used in the LDT may be distinguished from words via nonsemantic strategies such as familiarity (Balotta & Chumbley, 1984). Indeed, a number of investigators have reported longer reaction times for lexical decisions as nonword foils appear increasingly word-like (e.g., pseudo homophones, Stone & Van Orden, 1993; Shulman & Davidson, 1977; James, 1975), and thus, presumably, require more semantic processing to be distinguished from real words. Most recently, the ability of lexical decision reaction times to track automatic semantic activation has been questioned (Heil, Rolke, & Pecchinenda, 2004).

An alternative task that more clearly taps semantic knowledge with less potential for heuristic-based processes is reading. Behavioral studies using reading as a dependent measure (e.g., pronunciation) have shown that it differs from the LDT in important ways: It is easier, as evidenced by the LDT's average error rate of 20%, and it produces a different pattern of priming results (see Neely, 1991 for a review comparing the two tasks). Reading is also less likely to engage strategies such as semantic matching (i.e., are the prime and target words related in meaning? Neely & Keefe, 1989), which may occur with the LDT despite brief SOAs (Chwilla, Hagoort, & Brown, 1998; De Groot, 1984). In addition, words with multiple meanings result in faster lexical decisions but slower reading times. This suggests that multimeaning ambiguity compromises a level of semantic comprehension inherent in reading that is not required by lexical decision (Piercey & Joordens, 2000). Thus, reading may rely more heavily on semantic processes than the LDT. In sum, reading offers two significant advantages to the LDT: (1) a clearer reliance on semantics and (2) fewer extraneous, nonsemantic cognitive processes. Silent reading is particularly well suited for fMRI as it eliminates the neural activity associated with making an overt motor response.

We sought to identify brain regions that were modulated automatically, by related concepts, while eliminating perceptual confounds and contamination from explicit tasks. In addition, we included an identity condition in order to compare adaptation effects with and without perceptual repetitions. An event-related paradigm combining rapid stimulus presentation (SOA = 250 msec) with a task that requires no overt response (silent reading) was designed to provide a stringent test for whether areas respond to conceptual as well as perceptual properties automatically. Participants underwent fMRI scanning while silently reading sequentially presented pairs of concrete nouns that were either unrelated, semantically related, or identical. Related pairs were defined as co-category exemplars (e.g., dog–horse) that were not strong associates of each other in order to ensure that both words were processed semantically rather than one simply triggering the other due to being regularly paired in the lexicon (e.g., black–white, salt–pepper; Moss & Tyler, 1995). Unrelated pairs were two nouns from different categories (e.g., mouse–table). We predicted more efficient

processing, as indexed by a decrease in the hemodynamic response, for identical word pairs in comparison to two unrelated words. Most importantly, we predicted pure semantic priming in the ventral temporal cortex as indexed by reduced activity for related compared to unrelated word pairs.

RESULTS

Behavioral Study

A behavioral study with 18 volunteers (none of whom participated in the imaging study) verified that semantic priming could be detected with a 250-msec SOA. In order to make the conditions as similar as possible to those in the fMRI study, the dependent measure was time to read the second word of each pair aloud (voice-onset time). Under the constraints of providing a measurable behavioral response, reading the second word aloud was the most similar task to silent reading. Errors were relatively rare and did not differ significantly across the three conditions [$F(1,18) = 1.25$, *ns*]. As predicted, voice-onset times differed significantly across conditions and were best modeled by a linear contrast. Relative to reading the second word of unrelated pairs ($M = 747$ msec), subjects were faster in response to related pairs ($M = 734$ msec), and showed the greatest facilitation for identical pairs [$M = 692$ msec; $F(1,18) = 37.05$, $p < .0001$].

fMRI Results

The imaging data were submitted to a random-effects ANOVA to determine how the relationship between word pairs modulated activity in different cortical regions. First, we used a stringent statistical criterion to identify all brain regions responding more to reading word pairs than to the visual fixation intervals ($p < 10^{-6}$). We then identified which of these regions showed *any* differential modulation between word-pair types (i.e., main effect of priming condition, $p < .01$). Masks of these areas then were applied to each individual's functional scans to extract the time series for each condition. This approach allowed an unbiased examination of the data without constraints from a priori hypotheses (i.e., without constraints on the ordering of the conditions).

Identity Priming

Consistent with previous research, several cortical areas showed repetition suppression for identical pairs relative to unrelated pairs (see Table 1) including the left ventral temporal cortex, centered on the fusiform gyrus, our primary area of interest. Although identical word pairs inherently include both visual and semantic repetition, of primary interest was whether semantically related, but visually different, word pairs would produce reduced activity in comparison to two unrelated words. This comparison would answer the central question that motivated this study: Is the ventral temporal cortex automatically modulated by semantic information?

Semantic Priming

Relative to unrelated word pairs, semantically related pairs were associated with reduced activity in several areas including the bilateral ventral temporal cortex, again centered on the fusiform gyrus (see Table 1; Figure 1). In the left ventral temporal cortex, this reduction was significant but smaller than that observed for identical pairs (i.e., unrelated > related > identical). A similar pattern was also observed in an anterior portion of the left inferior frontal cortex (centered at Talairach coordinates: $x = -38$, $y = 23$, $z = 16$; see Table 1; Figure 1), an area often identified in semantic and conceptual processing tasks (see Bookheimer, 2002, for a review).

In contrast to this expected pattern of results, three areas showed greater reductions for semantically related pairs compared to identical pairs: a posterior portion of the left inferior frontal gyrus, the left postcentral gyrus, and the right medial occipital cortex (see Table 2). That is, these areas responded *less* to within-category, semantically related repetitions compared to the same word twice (i.e., within-category, identical repetitions). The largest area to show this effect was a right medial extrastriate area immediately superior to the anterior portion of the calcarine sulcus.

Animate Objects versus Manipulable Artifacts

The present study utilized 20 categories of objects. Of these categories, five were clearly representative of animate things (four-footed animals, fish, birds, insects, and body parts) and five were clearly representative of manipulable artifacts (tools, kitchen utensils, toys, weapons, and musical instruments). The use of both artifact and animate pairings therefore afforded a gross comparison between these two domains (power constraints prohibited examining priming within these two domains). This comparison was motivated by previous research that has found anatomical dissociations between the perception of animate and manipulable, artifact stimuli such as common tools (see Thompson-Schill, 2003; Bookheimer, 2002; Martin & Chao, 2001, for reviews).

A direct comparison between word pairs denoting animate and manipulable artifacts revealed a number of regions showing greater activity for animate objects relative to manipulable artifacts. These regions included the lateral extent of the fusiform gyri bilaterally, the right superior temporal sulcus (STS), the left superior tem-

Table 1. Local Maxima within Areas Demonstrating Reduced BOLD Signal for Identical Pairs Relative to Unrelated Pairs, Related Pairs Relative to Unrelated Pairs, and Identical Pairs Relative to Related Pairs

			Unrelated > Identical				*Unrelated > Related*				*Related > Identical*			
			Talairach Coordinates				*Talairach Coordinates*				*Talairach Coordinates*			
ROIs	*vml*	*BA*	*x*	*y*	*z*	*t*	*x*	*y*	*z*	*t*	*x*	*y*	*z*	*t*
Frontal Lobe														
Left inferior frontal gyrus (anterior)	2109	46	−38	23	16	4.81	−38	23	14	3.14	−35	21	16	2.16
Left inferior frontal gyrus (posterior)	1477	6/9	−34	7	25	3.45	−41	3	24	4.32				
			−34	15	26	3.78								
Temporal Lobe														
Left ventral temporal cortex	4430	37	−34	−55	−4	5.14	−37	−57	−8	3.40	−36	−53	−4	3.23
			−32	−45	−12	4.64	−32	−42	−12	3.06	−30	−46	−11	2.07
Right ventral temporal cortex	1266	37	38	−60	−4	3.89	38	−57	−6	3.59				
Parietal Lobe														
Left postcentral gyrus	1266	3/4	−54	−16	27	3.01	−55	−17	25	4.08				
Occipital Lobe														
Left cuneus	422	31	−23	−78	24	3.23	−26	−77	24	3.36				
Left middle occipital gyrus	2461	19	−38	−69	4	4.12	−42	−70	6	2.65	−37	−66	2	2.26
Left calcarine sulcus	633	19	−23	−66	3	2.82	−18	−68	4	3.81				
Right middle occipital gyrus	492	19/31	30	−75	17	2.26	30	−76	17	3.46				
Right middle occipital gyrus	1195	37/19	44	−70	4	4.01	49	−71	7	2.95				
Right precuneus	844	19	26	−69	34	3.60	26	−72	38	3.63				
Right calcarine sulcus	5203	18					20	−67	13	4.39				

Areas were defined by a random-effects ANOVA as being more active for Reading > Fixation ($p < 10^{-6}$) and showing any modulation by pair type ($p < .001$). Pairwise comparisons within these areas produced the foci listed below.

vml = volume in microliters (1 mm^3); BA = Brodmann's area.

poral gyrus (STG), the anterior extent of the calcarine sulcus, and the prefrontal cortex, bilaterally (see Table 3). In contrast, manipulable artifact pairs showed greater activity in the bilateral inferior parietal cortex, the left anterior cingulate and left premotor cortex, relative to animate pairs (see Figure 2).

DISCUSSION

Overall, our findings are consistent with a large and ever-growing body of literature showing repetition related decreases of the BOLD signal. In addition, they extend this finding of hemodynamic repetition suppression to a word-pair paradigm in which the delay between items was only 100 msec. Thus, both very short delays (on the order of milliseconds), and very long delays (on the order of days; van Turennout, Bielamowicz, & Martin, 2003; Chao, Weisberg, & Martin, 2002; van Turennout, Ellmore, & Martin, 2000; Wagner, Maril, & Schacter, 2000) between the first and second presentations of an item produce hemodynamic repetition suppression effects.

Most importantly, we identified several regions in which neural activity was modulated by word-pair type in a manner that mirrored the behavioral semantic priming effect (unrelated > related > identical as measured by voice-onset time). Specifically, relative to reading unrelated word pairs, activity in the ventral temporal and left inferior frontal cortices was significantly reduced for semantically related pairs, and was further reduced when reading the same word twice. This pattern is exactly what one would expect given the assump-

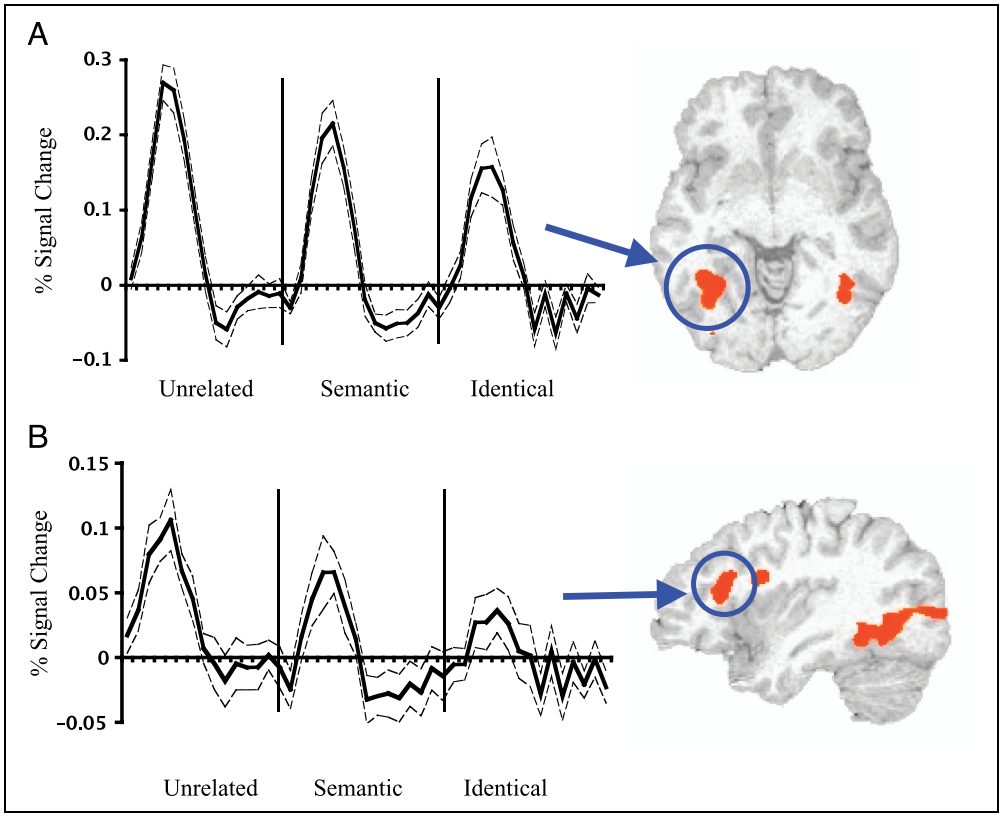

Figure 1. The left ventral temporal cortex (A) and the left inferior prefrontal cortex (B) showed the greatest activity for unrelated pairs, less for semantic repetitions, and the least for identical repetitions. ROIs were defined by a random-effects ANOVA as responding more to reading than to fixation ($p = 10^{-6}$) and showing any modulation between word-pair conditions ($p < .01$). These ROIs produced an averaged time series across subjects for each condition. Dashed lines represent standard error around the mean. Tick-marks on the *x*-axis represent seconds (15 sec per condition).

tion that priming (a repetition-related performance facilitation) is associated with reduced neural activity relative to an appropriate control condition. Thus, we take these findings as providing strong evidence that the posterior region of the fusiform gyrus of the temporal lobes and the left inferior frontal cortex are critical nodes in a neural system for representing the meaning of concrete objects.

The finding that the ventral temporal cortex, especially in the left hemisphere, was strongly activated during word reading, and that this activity was reduced for semantically related word pairs relative to unrelated pairs, is consistent with Koutstaal et al.'s (2001) finding for object exemplar priming and supports their interpretation that this area is involved in conceptual processing. This finding is also consistent with a large number of neuroimaging studies (see Martin, 2001, for review) and neuropsychological investigations (e.g., Sharp, Scott, & Wise, 2004) on the role of the ventral temporal cortex in representing conceptual knowledge.

In addition to the ventral cortex, two areas in the LIPFC demonstrated semantic priming. The LIPFC is now considered to be a heterogeneous area comprising a dorsal region (BA 44/45) associated with phonology and one (or possibly two) anterior ventral area (BA 47/45; Bookheimer, 2002; Poldrack et al., 1999) associated with a variety of semantic tasks (e.g., with visual stimuli, Wagner, Desmond, et al., 1997; Vandenberghe et al., 1996; for semantic decisions about words, Wagner, Schacter, et al., 1998; Gabrieli et al., 1996; Demb et al., 1995; Kapur et al., 1994; word generation on the basis of semantic relationships, Klein, Milner, Zatorre, Meyer, & Evans, 1995; Petersen, Fox, Snyder, & Raichle, 1990). In addition, this anterior area is widely held to be a semantic executive system recruited when access to long-term semantic memory is required by task demands (Roskies, Fiez, Balota, Raichle, & Petersen, 2001; Fiez, 1997, Hagoort, 1997; Wagner, Desmond,

Table 2. Local Maxima within Areas Demonstrating Reduced BOLD Signal for Related Pairs Compared to Identical Pairs

	Related > Identical					
ROIs	*vml*	*BA*	*x*	*y*	*z*	*t*
Frontal Lobe						
Left inferior frontal gyrus (posterior)	1477	6/9	−45	3	24	2.81
Parietal Lobe						
Left postcentral gyrus	1266	40	−58	−21	24	3.23
Occipital Lobe						
Right calcarine sulcus	5203	18	22	−66	15	3.38

vml = volume in microliters (1 mm^3); BA = Brodmann's area.

et al., 1997). However, although the LIPFC is more active during explicit semantic tasks compared to nonsemantic tasks, this region also shows decreased activity for repeated semantic processing (Demb et al., 1995) and semantic repetition priming (Rossell et al., 2003). The co-localization of processing-related increases and repetition-related decreases may reflect a common neural substrate that aids in semantically encoding incoming verbal information *and* requires less neural computation when that item is repeated (Demb et al., 1995).

The Specter of Controlled Processes

Although our data provide strong evidence that activity in ventral temporal and frontal regions is modulated by semantic relatedness, the extent to which this finding reflects ''automatic'' semantic processes can be questioned. As reviewed in the Introduction, a word-reading task coupled with a short SOA provides a simple paradigm for eliciting automatic semantic activation and clearly has advantages over the LDT used in previous neuroimaging studies. Nevertheless, although word reading occurs with little effort in adult readers, and our task did not require subjects to perform any additional task, this does not necessarily prevent other processes from occurring after the words have been read. This concern is particularly relevant for fMRI studies because the BOLD response develops on the order of seconds. As a result, it is possible that controlled processes (such as semantic matching) may have occurred after the presentation of a word pair. If a controlled process occurred and if it varied systematically with relatedness (e.g., if semantic matching is more difficult for unrelated words than related pairs), one would expect similar modulation to that observed. However, although the effect of postword recognition controlled processes cannot be ruled out, there are several reasons why these processes are unlikely to have been major determinants of our findings. First, the evidence suggests that subjects do not engage in semantic matching—one of the primary postword recognition strategies—during simple word reading with short SOAs (<300 msec; Neely, 1991; Neely & Keefe, 1989; but see Brown, Hagoort, & Chwilla, 2000). Second, the rapid event-related design with intermixed conditions allowed for the fast-paced presentation of a large number of word pairs (480) with word pairs from each condition presented in a pseudorandom order. In order for a postrecognition controlled process to generate the results presented, subjects would have needed to spontaneously develop and engage in the same effortful postrecognition process after nearly every trial. Given the experimental design, the likelihood that such a process occurred consistently across subjects and trials is slim.

Similar arguments apply to the possibility that subjects generated an explicit visual image of each object in the word pair. First, as noted above, our design would seem to discourage such an effortful strategy. Second, why explicit generation of visual images of objects would produce the observed pattern of reduced activity as a function of semantic relatedness is not directly obvious. Indeed, Giesbrecht, Camblin, and Swaab (2004) demonstrated that the semantic relatedness of word pairs did not interact with their imageability (high vs. low). It is important to stress that we are *not* suggesting that visual imagery (i.e., retrieving stored information about what an object looks like) played no part in producing the pattern of results we observed in our study. To the contrary, we expect that it was the retrieval of visual information about the objects that was primarily responsible for the activations we observed in the fusiform gyrus. For example, it may be that the visual image of an object is automatically retrieved as an unconscious and obligatory by-product of normal word reading. In that case, automatic, implicit generation of an object image would be the mechanism by which we access an important property underlying the meaning of words denoting concrete entities. In this sense, implicit visual imagery would be an obligatory component of reading for meaning. However, we are arguing against the idea that our results for the fusiform gyrus could be readily explained by the nonobligatory, explicit generation of visual object images that occurred *after* the word's meaning had been determined. There is little reason to expect that engaging in this strategy, as well as engaging other postrecognition controlled processes, would occur given the constraints of our design.

Our results suggest that automatic semantic priming occurs and is associated with hemodynamic decreases in ventral temporal and left inferior frontal cortices. However, additional research is clearly needed to more completely rule out the contribution of controlled processes. Masked priming paradigms, in which the subject is unaware of the prime, and thus, cannot explicitly process the semantic relationship between prime and target, will be particularly useful in addressing this vexing problem (Dehaene et al., 2001; Perea & Gotor, 1997).

Less Activity for Related than Identical Word Pairs

Unexpectedly, three areas (the left postcentral gyrus, a left inferior frontal area, and the right calcarine sulcus) showed less activity for semantically related pairs (e.g., lion–dog) compared to identical repetitions (lion–lion). This suggests, perhaps paradoxically, that these areas operated more efficiently when encountering a related stimulus compared to when encountering the same stimulus twice (and see Neely, VerWys, & Kahan, 1998, for behavioral evidence for semantic but not identity priming under certain conditions). Although it is possible that lion–dog is more categorically rich than lion–lion, it is not clear how this would result in less activity

Table 3. Local Maxima within Areas Demonstrating Greater BOLD Signal for Animate Relative to Artifact Pairs and Artifact Relative to Animate Pairs

			Animate > Artifact				*Artifact > Animate*			
			Talairach Coordinates				*Talairach Coordinates*			
Region	*vml*	*BA*	*x*	*y*	*z*	*t*	*x*	*y*	*z*	*t*
Frontal Lobe										
Left superior frontal gyrus	1332	10	−17	60	7	5.42				
	110	8	−5	40	46	3.61				
Left middle frontal gyrus	522	46	−42	34	21	2.39				
Left precentral gyrus (premotor)	106	4/6					−47	−7	34	−3.10
Left anterior cingulate gyrus	129	24					−4	36	7	−3.61
	130	32					−8	16	39	−2.58
Left medial frontal gyrus	192	10	−5	55	−4	2.84				
Right superior frontal gyrus	165	6					13	1	55	−3.10
Right medial frontal gyrus	245	8	3	25	53	3.10				
Right inferior/middle frontal gyrus	496	9	54	15	33	3.61				
Temporal Lobe										
Left lateral fusiform gyrus	5692	37	−47	−64	−8	5.42*				
Left superior temporal gyrus	187	42	−58	−29	10	2.84*				
Right lateral fusiform gyrus	2256	37	44	−62	−10	3.87*				
			41	−54	−18	2.84*				
Right superior temporal sulcus	402	22	60	−37	7	3.10				
	399		47	−55	18	3.10				
Right angular gyrus	373	39	47	−65	32	3.10				
Parietal Lobe										
Left inferior parietal lobe	134	40					−38	−39	24	−3.36
Left precuneus	1172	7	−23	−71	53	4.39				
Left postcentral gyrus	279	7	−1	−46	66	4.91				
Right inferior parietal lobe	274	40					38	−34	43	−3.61*
	110	40	55	−31	27	2.84				
Right superior parietal lobe	183	7	36	−65	54	3.61*				
Right precuneus	6703	7	6	−79	46	6.20*				
Right posterior cingulate gyrus	4058	29	1	−46	11	5.42*				
Occipital Lobe										
Left middle occipital gyrus (medial)	187	18	−10	−94	14	3.61				
Left middle occipital gyrus (lateral)	549	19	−40	−75	14	3.61*				
Right middle occipital gyrus	299	18					25	−87	2	−3.10*

Table 3. *(continued)*

			Animate > Artifact				*Artifact > Animate*			
			Talairach Coordinates				*Talairach Coordinates*			
Region	*vml*	*BA*	*x*	*y*	*z*	*t*	*x*	*y*	*z*	*t*
Medial lingual gyrus	2655	18	1	−78	10	4.39*				
Medial calcarine cortex	1617	18	2	−65	2	3.61*				
Cerebellum										
Right	414		33	−67	−33	3.87				
Left	198		−18	−70	−34	5.16				
	112		−5	−73	−32	4.65				

*Areas larger than 100 mm^3 that were significant for the pairwise comparison (animate vs. artifact words) at $p < .05$ as determined by a fixed-effects group map thresholded by reading > fixation, $p < 10^{-6}$.

Indicate areas significant at $p < .05$ for the same pairwise comparison as determined by a random-effects ANOVA thresholded by reading > fixation, $p < 10^{-6}$.

for related than identical pairs. Both left hemisphere areas also showed significant reductions for identical repetitions albeit to a lesser extent than those associated with semantic repetitions. However, the large area in the right medial extrastriate cortex activated as strongly for identical pairs as unrelated pairs, with reductions solely for semantically related (but visually different) pairs. Categorical processing has been associated with the right hemisphere (e.g., impaired co-category exemplar priming in patients with right hemisphere lesions, Hagoort, Brown, & Swaab, 1996; categorical information processing, Chiarello & Richards, 1992) and, indeed, at an almost identical locus (categorically related words compared to associatively related words; Kotz et al., 2002). Why an area that is potentially involved in categorical processing would yield less activity for two different co-category exemplars rather than the same exemplar twice (identical repetition) remains a puzzling question for future research.

Animate versus Artifact Concepts

The current study allowed us to examine, at a gross level of distinction, the automatic processing of animate versus artifact word pairs. Previous studies have documented a dissociation between the STS, which responds preferentially to animate objects and their associated patterns of flexible, articulated motion, and the MTG, which prefers manipulable objects and the rigid, unarticulated motion vectors associated with this object type (Beauchamp, Lee, Haxby, & Martin, 2003; Beauchamp, Lee, Haxby, & Martin, 2002). Similarly, the more lateral region of the posterior fusiform gyrus responds preferentially to animate stimuli (e.g., faces, animals), whereas the medial portion responds preferentially to inanimate stimuli (e.g., tools; Chao et al., 1999). A number of patient (Tranel, Damasio, Eichorn, et al., 2003; Tranel, Damasio, & Damasio, 1997) and imaging studies (Chao et al., 1999; Martin et al., 1996; Perani et al., 1995; see Martin, 2001, for review) also have implicated the medial occipital cortex, including the calcarine sulcus, in the processing of animate compared to inanimate (artifacts) stimuli. Although some have argued that this area is responding to visual complexity rather than animacy per se (Moore & Price, 1999), it also demonstrates greater activity for animals than for tools when items are shown in silhouette (Martin et al., 1996). Finally, given the manipulable nature of items selected for the artifact stimuli in the current study, regions associated with grasping and manipulating objects such as the left premotor cortex and the posterior parietal cortex around the intraparietal sulcus were expected to be more active for artifact relative to animate pairs (Beauchamp, Lee, Haxby, & Martin, 2003; Culham et al., 2003; Kellenbach, Brett, & Paterson, 2003; Chao & Martin, 2000; Chao et al., 1999).

Consistent with these findings, the lateral portion of the fusiform gyri, the right STS, and the right calcarine sulcus were more active for animate relative to manipulable artifact word pairs (along with several prefrontal areas). In contrast, relative to animate word pairs, manipulable artifacts (toys, tools, kitchen utensils, musical instruments, and weapons) produced greater activity in the bilateral inferior parietal lobule (IPL), the left premotor cortex, and the left cingulate gyrus. The finding that word pairs referring to animate objects activated more posterior and ventral areas, whereas artifact pairs activated anterior and dorsal areas, provides additional support for the claim that conceptual knowledge about these object categories are represented in these regions.

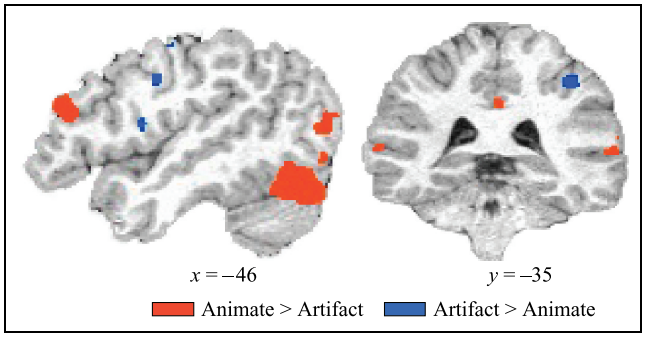

Figure 2. Direct comparison between animate and artifact word pairs. Several areas showed greater activity (red areas) for animate relative to artifact pairs. These included the lateral extent of the left fusiform gyrus (see sagittal view) and the bilateral STS (see coronal view) and medial occipital cortex (not shown). Artifact pairs showed greater activity (blue areas) in the left premotor cortex (sagittal view) as well as the bilateral inferior parietal lobules (right IPL, coronal view) and left anterior cingulate (not shown).

Conclusion

The present study revealed repetition-related reductions in the ventral occipito-temporal cortex for rapidly presented semantically related word pairs, providing strong support that this area is automatically modulated by conceptual properties. Reduced activity was also observed in the LIPFC for related compared with unrelated word pairs, suggesting that this area is engaged during automatic as well as controlled processing of semantic information. In addition, categories used in the present study allowed us to compare activation elicited by word pairs referring to animate things with those referring to manipulable artifacts. Relative to manipulable artifact words, animate words produced greater activity in the lateral fusiform gyri, the right STS, and the medial extrastriate cortex. Conversely, artifact pairs were associated with greater activity in the left premotor cortex, the left anterior cingulate, and the bilateral IPL. These findings provide further evidence that object concepts are distributed in discrete cortical regions associated with sensory and motor systems. Finally, our findings add to a growing literature on the utility of adaptation paradigms to probe the processing characteristics of specific cortical regions.

METHODS

Behavioral Study

Participants

Behavioral data were collected from 18 normal volunteers (8 men). All subjects were right-handed as determined by the Edinburgh Handedness Scale; spoke English as their first language; had normal or corrected-to-normal visual acuity, no known history of neurological impairments or reading/vocabulary difficulties. Participants were financially compensated for their participation according to NIH guidelines.

Materials

The stimuli included 400 concrete nouns selected from 20 categories (birds, body parts, clothing, fish, flowers, four-footed animals, fruit, furniture, insects, kitchen utensils, musical instruments, natural earth formations, parts of buildings, tools, toys, trees, types of dwellings, vegetables, vehicles, weapons; Battig & Montague, 1969). Twenty single words from each category were selected to create identical, semantically related (items from the same-object category; e.g., dog–lion), and unrelated word pairs (from different-object categories; e.g., mango–chair). Over the course of the experiment, the subject read 160 word pairs within each condition for a total of 480 word pairs. The first four runs used unique combinations of all the words. In order to obtain an adequate number of trials for the fMRI study, all words were repeated once over the remaining four runs. All repeat words were randomly assigned to a different condition than the one in which the word was previously presented in order to cancel out potential repetition effects across conditions. Within-pair order was counterbalanced so that if a word appeared as the first word in a pair during the first four runs, that word appeared as the second word in a different pair during the last four runs.

Words were balanced for length (M_i = 5.63, M_r = 5.63, M_u = 5.66) and frequency (M_i = 24.80, M_r = 25.30, M_u = 24.02; Kucera & Francis, 1967) across identical, related, and unrelated word pairs, respectively. In addition, words were balanced for length within pairs to

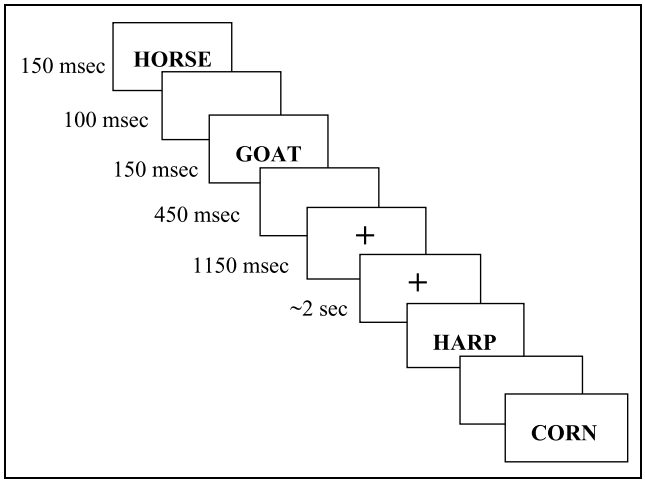

Figure 3. Time-line of the experiment. Subjects in the behavioral study were asked to read the second word of every pair aloud, as quickly and accurately as possible. Subjects in the fMRI study were instructed to silently read words as they appeared. Word-pair types [identical, related (same category), unrelated] were pseudorandomly intermixed in both studies.

avoid focal widening/constriction between prime and target (e.g., axe–saw, not axe–screwdriver). Semantically related word pairs were never high associates of each other (e.g., lion–dog, not cat–dog) nor were unrelated pairs (e.g., river–chair, not river–bed). Similarly, the last word in a pair was never a high associate of the first word in the next pair. In addition, no related or unrelated word pairs contained identical letter strings (e.g., house–camel, not house–mouse) so as to avoid any visual form repetition in these conditions.

Animate pairs included all identical and related pairs within the categories: body parts, insects, fish, birds, and four-footed animals. Manipulable artifact pairs were defined as all identical and related pairs within the categories: weapons, toys, musical instruments, kitchen utensils, and tools (see Appendix for examples). Both animate and artifact conditions had 80 pairs (40 identical, 40 related).

Procedure

Subjects were instructed to silently read the first word of every pair but to read the second word aloud as fast and as accurately as possible. Words appeared serially, in black type against a white background. The first word of each pair appeared for 150 msec followed by a 100-msec blank white screen and then a second word appeared for 150 msec. This word-pair sequence was followed by a blank screen for 450 msec and then a fixation cross for 1150 msec. Thus, the total word-pair event lasted for 2000 msec. Word-pair types were presented in an intermixed pseudorandom order, with a fixation cross presented during a variable intertrial interval (range ITI 0–13 sec, mean = 2.6 sec; see Figure 3). Presentation order was optimized for later hemodynamic response estimation (Cox, 1996). Voice-onset times were recorded by Superlab (Chase & Abboud, 1997).

fMRI Study

Participants

Fifteen normal volunteers (8 men) who had not taken part in the behavioral study participated in the fMRI experiment. All subjects were right-handed as determined by the Edinburgh Handedness Scale; spoke English as their first language; had normal or corrected-to-normal visual acuity, no known history of neurological impairments or reading/vocabulary difficulties. Participants were financially compensated for their participation according to NIH guidelines.

Materials and Procedure

The stimuli and the presentation parameters were identical to those used in the behavioral study. However, subjects were instructed to silently read both words of the word pairs rather than saying the second word aloud. Subjects lay supine in the MRI scanner and stimuli were back-projected onto a screen in front of them. Participants viewed the display via tilted mirrors placed above their eyes.

Imaging Parameters

High-resolution SPGR anatomical images (124 sagittal slices, 1.2-mm thick, field of view [FOV] = 24 cm, acquisition matrix = 256 × 256) and functional data (gradient-echo, echo-planar imaging sequence, repetition time [TR] = 2 sec, echo time [TE] = 30 msec, flip angle = 90°, 24 contiguous 5-mm axial slices, voxel size 3.75 × 3.75 × 5 mm) were acquired on a 3-T GE scanner.

Imaging Analysis

Functional and anatomical images were analyzed with AFNI (Cox & Hyde, 1997; Cox, 1996). Functional images were motion corrected and smoothed with a 4.5-mm full-width half-maximum Gaussian filter. Individual subject maps, both anatomical and functional, were normalized to the standardized space of Talairach and Tournoux (1988). Responses to single word pairs from each stimulus category were calculated without assumptions about the temporal dynamics of the hemodynamic response. Delta functions representing the response at 1-sec intervals in a 15-sec window following stimulus presentation were fit to the MR signal. For the main comparisons, a random-effects ANOVA was performed on the mean of the four time points that typically surrounded the peak activation for each condition (seconds 3–6 in each 15-sec estimated hemodynamic response). The resulting group activation map was thresholded such that only voxels which (a) responded more to words than fixation ($p < 10^{-6}$) and (b) showed *any* modulation between conditions ($p < .01$) survived. All surviving activation clusters larger than 5 contiguous voxels provided the template for regions-of-interest (ROI) masks. These masks were then applied to each individual's data to extract the average hemodynamic response for each condition within each ROI. The means of the peaks for each condition for each subject were submitted to an ANOVA and pairwise comparisons were performed to determine significant differences between conditions. Due to the reduced number of word pairs referring to animate or manipulable artifacts, a fixed-effects analysis was used to evaluate possible category-related differences. This group activation map was thresholded such that only voxels which (a) responded more to words than fixation ($p < 10^{-6}$) and (b) showed a difference ($p < .05$) between the two categories survived. Activations listed in Table 3 with asterisks also survived a random-effects analysis for this comparison.

APPENDIX

Examples of Word Pairs by Priming Condition

Identical	*Related*	*Unrelated*
crow–crow	banana–apricot	skirt–rattle
jacket–jacket	table–bench	ravine–strainer
puppet–puppet	daisy–lilac	celery–giraffe
cucumber–cucumber	pig–fox	hat–gun
sword–sword	rifle–arrow	spoon–bench
volcano–volcano	car–jet	river–brain
pansy–pansy	flea–worm	desk–lion
orange–orange	fork–cup	castle–violet
flute–flute	cave–hill	elevator–mackerel
table–table	bugle–violin	ankle–carrot

Examples of Word Pairs by Animate and Artifact Categories

Animate	*Artifact*
tuna–clam	banjo–harp
neck–foot	sword–sword
tongue–tongue	rifle–arrow
goldfish–goldfish	skillet–skillet
camel–camel	crayon–balloon
beetle–beetle	jacks–jacks
horse–goat	fork–cup
pigeon–pigeon	pliers–pliers
vulture–falcon	skillet–skillet
flea–worm	axe–saw

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Reprint requests should be sent to Thalia Wheatley, Laboratory of Brain and Cognition, National Institute of Mental Health, National Institutes of Health, 10 Center Drive MSC 1366, Bethesda MD 20892, or via e-mail: wheatley@nih.gov.

The data reported in this experiment have been deposited with the fMRI Data Center archive (www.fmridc.org). The accession number is 2-2005-118W5.

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