

Separable Effects of Semantic Priming and Imageability on Word Processing in Human Cortex

Barry Giesbrecht¹, C. Christine Camblin² and Tamara Y. Swaab^{1,3}

¹Center for Mind & Brain, University of California, One Shields Avenue, Davis, CA 95616, USA, ²Department of Psychological & Brain Sciences, Duke University, Durham, NC, USA and ³Department of Psychology, University of California, Davis, CA, USA

Understanding the neural representation of semantic concepts is at the core of understanding human knowledge and experience. Competing cognitive theories suggest that these neural representations are based on either a unitary semantic code or on multiple semantic codes. We contrasted these theories using event-related fMRI in a semantic priming study. Pairs of words were presented that were either semantically related or unrelated and were either high or low imageable. The unitary view predicts that there should be little or no difference between neural activity evoked by high and low imageable words when presented in a related context, but large differences in neural activity when there is an unrelated context. In contrast to this view, we provide evidence for functionally and anatomically separable effects of context and imageability in human cortex, suggesting that semantic knowledge consists of multiple representational codes.

Keywords: fMRI, imageability, priming, semantic memory

Introduction

Conceptual and semantic representations reflect our knowledge of events, objects and states in the real world. There have been many empirical investigations into the cognitive and neural architectures of semantic representations, but the exact nature of these representations is a matter of much debate. Specifically, it remains unresolved whether semantic information is organized as a unitary system that utilizes a single verbally based (Caramazza *et al.*, 1990) or perceptually based (Barsalou, 1991; Barsalou *et al.*, 2003) representational code, or whether different types of semantic information are stored as separate perceptual and verbal codes (Warrington and McCarthy, 1987; Shallice, 1988; Paivio, 1991). Empirical evidence from behavioral studies, electrophysiological studies, and studies in patients with brain lesions has been marshaled in support of each of these viewpoints (Kieras, 1978; Schwanenflugel and Shoben, 1983; Warrington and McCarthy, 1987; Paivio, 1991; Caramazza and Shelton, 1998; Holcomb *et al.*, 1999; Kiehl *et al.*, 1999; Jessen *et al.*, 2000; West and Holcomb, 2000; Miceli *et al.*, 2001; Swaab *et al.*, 2002). In the current study we used functional magnetic resonance imaging (fMRI) to investigate the brain's organization of semantic knowledge. In this regard, one main question will be addressed: Are specific and separable brain circuits involved in the processing of verbal-based and image-based representations of words?

Functional neuroimaging and neuropsychological studies investigating the neural architecture of the semantic system have focused mainly on identifying the brain structures that might represent category specific knowledge (Caramazza and Shelton, 1998; Martin and Chao, 2001), and more generally on establishing which structures comprise the semantic network.

Three cortical areas of the left hemisphere have been consistently cited as being critical to processing semantic information. These areas include: left inferior prefrontal cortex (LIPC) (Buckner and Koustaal, 1998; Poldrack *et al.*, 1999; Buckner *et al.*, 2000; Wagner *et al.*, 2000, 2001; Donaldson *et al.*, 2001; Dobbins *et al.*, 2002; Gold and Buckner, 2002), including anterior LIPC (aLIPC), encompassing Brodmann's areas (BA) 45/47, and posterior LIPC (pLIPC) near Broca's area (BA 44); left middle temporal gyrus (LMTG; BA 20/21) (Martin and Chao, 2001; Chao *et al.*, 2002; Gold and Buckner, 2002); and left parietal cortex (Schacter and Buckner, 1998; Poldrack *et al.*, 1999; Gold and Buckner, 2002), including the inferior parietal lobe (LIPL) and the supramarginal gyrus (LSMG), both encompassing BA 40. Although there is little controversy that these areas are involved in the semantic system, their precise function is a matter of debate. For example, there are at least three different models that posit a specific role for LIPC in semantic processing (Thompson-Schill *et al.*, 1997, 1998, 1999; Poldrack *et al.*, 1999; Wagner *et al.*, 2000, 2001; Gold and Buckner, 2002). However, none of these models address the question of whether there are single or multiple semantic codes.

The present study investigated the organization of semantic knowledge and whether the semantic system supports single or multiple codes by examining the so-called '*concreteness effect*'. It has been well established that concrete, high imageable, words such as '*banana*' are more easily understood than abstract, low imageable, words such as '*justice*'. Two major theories have been proposed to explain this effect of imageability, and these theories make specific claims about the role of the linguistic context on the processing of high and low imageable words. According to one theory, there are two separate semantic systems, one based on verbal codes and the other based on image codes. This so-called '*dual coding hypothesis*' (Paivio, 1991) posits that the concreteness effect or effect of imageability arises because high imageable words draw on both verbal and image-based codes, whereas low imageable words activate only the verbal codes. In contrast, the '*context availability hypothesis*' does not propose the existence of separate semantic systems (Kieras, 1978; Schwanenflugel and Shoben, 1983), but explains the effect of imageability by hypothesizing that high imageable words are more closely linked to relevant contextual knowledge within a single semantic memory store. High imageable words can therefore activate more semantic information than low imageable words, and it is this increased activation that causes facilitated processing (for a complete discussion of the close relationship between concreteness and imageability, see Richardson, 1975).

One approach to testing these single versus dual code models and to studying the organization of semantic representations has been to determine whether different brain areas are involved in processing concrete and abstract words. For instance, neuropsychological studies have provided results that seem compatible with the idea that separable brain areas are involved in the processing of abstract and concrete words. Many aphasic patients and deep dyslexic patients with lesions in the left hemisphere show poorer performance on abstract than concrete words (Goodglass *et al.*, 1969; Coltheart, 1980; Martin, 1996). In addition, there have been case reports of patients that showed the reverse pattern, that is selective impairments on concrete relative to abstract words (Warrington, 1975; Warrington and Shallice, 1984). Most of these latter patients suffered from bilateral damage to the inferior anterior temporal lobes. The results from these lesion studies have contributed to the idea that there may be an (additional) right hemisphere locus for the representation and processing of concrete words (Coltheart, 1980). Functional neuroimaging studies of healthy subjects have also provided support for a multiple representation account. For instance, early positron emission tomography studies reported more activity in LIPC when subjects read concrete words than when they read abstract words (Petersen *et al.*, 1988).

The neuropsychological and neuroimaging data mentioned above are in line with the dual-coding view. However, results of other neuroimaging studies have been interpreted as support for a unitary semantic representation as proposed by the context availability hypothesis (Kiehl *et al.*, 1999; Jessen *et al.*, 2000). For instance, Kiehl and colleagues (Kiehl *et al.*, 1999) failed to show a processing advantage for concrete words, consistent with the context-availability view. Thus, adopting the approach of simply identifying different brain areas involved in the processing of concrete high imageable and/or abstract words has provided support for both the dual coding and context availability views. It therefore remains an open question whether the imageability effect, and thereby the organization of the underlying semantic system, is supported by a single or multiple representational codes.

In the present study, the idea that words can be represented by more than one semantic code was tested more directly, by assessing whether the imageability effect is modulated by supporting contextual information. Here, the dual coding and context availability models make very specific and competing predictions about how effects of imageability should be modulated by the presence of a supporting context. According to the dual coding hypothesis, an effect of imageability should not be modulated by supporting context because regardless of context, high imageable words will always benefit from drawing on separate verbal and image-based codes, whereas low imageable words can only activate verbal codes. In contrast, according to the context availability hypothesis, the imageability effect should be modulated by context such that when high and low imageable words are preceded by equally supporting contexts, the effect of imageability or concreteness should diminish or disappear. Because high imageable words have strong internal contexts the processing of these words is not further facilitated by additional external context, whereas low imageable words lack strong internal context and hence benefit from external context to such a degree that they are processed as efficiently as high imageable words. Several event-related potential (ERP) studies have tested these hypo-

theses by attempting to identify interactions between context and imageability in terms of cortical activity, and unlike the results of the neuropsychological and neuroimaging investigations of the imageability effect mentioned above, the results of these ERP studies have been more consistent and in support for the dual coding view (Holcomb *et al.*, 1999; West and Holcomb, 2000; Swaab *et al.*, 2002). In particular, these studies either found no modulation of the imageability effect by supporting context (Swaab *et al.*, 2002), or effects of context on imageability that were in a direction opposite to what is predicted by the context-availability hypothesis (Holcomb *et al.*, 1999; West and Holcomb, 2000). Although these ERP measures of the cortical activity have a high temporal resolution, their spatial resolution is relatively coarse in comparison to functional magnetic resonance imaging (fMRI) measures of cortical activity. Hence, the precise neuroanatomical bases of the previous ERP effects of context and imageability remain unclear.

Here we used event-related fMRI to investigate the cortical organization of semantic knowledge and the nature of the underlying representations by testing whether the effects of imageability are modulated by supporting context in the healthy human brain. We used a typical two-word priming paradigm in which a prime word and a target word are presented sequentially on each trial and the task is to make a judgment about the target word (see Fig. 1a and Methods). Previous studies have demonstrated that behavioral responses are faster and the amplitude of the N400 (an ERP component sensitive to lexical integration and semantic relatedness) is reduced to target words that are preceded by a related prime word relative to targets preceded by an unrelated prime word, the so-called 'semantic priming effect' (Meyer *et al.*, 1975; Neely, 1977; Bentin *et al.*, 1985; Holcomb and Neville, 1990; Holcomb, 1993; Swaab *et al.*, 2002). In the present study, the semantic priming effect is used as a measure of sensitivity to context, thus the phrases 'semantic priming effect' and

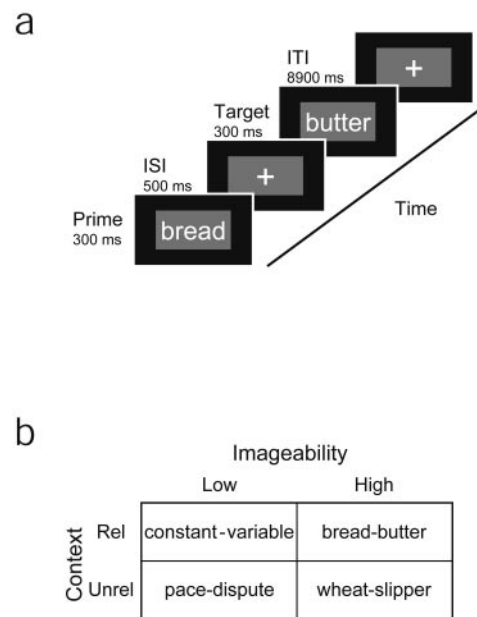


Figure 1. Priming task. (A) A schematic representation of the trial sequence. (B) Examples of the factorial combination of prime-target contextual (Related or Unrelated) relationship and imageability (Low and High).

'context effect' will be used interchangeably. Although neuroimaging studies have provided evidence for reduced neural activity to repeated words and pictures in extrastriate visual areas (Squire *et al.*, 1992; Buckner *et al.*, 1995), there are very few that provide evidence for similar reductions in the semantic system after single presentations of words that are primed by a different but contextually related word (cf. Rossell *et al.*, 2003).

There were two key manipulations in our task. First, context was manipulated by varying the relationship between the prime and the target words in each pair. That is, the target word was either related or unrelated to the prime word. Second, half of the word pairs were high imageable and half were low imageable (see Fig. 1*b* for examples). In this way we were able to investigate the imageability effects on target words when the context was supporting (related condition), and when the context was not supporting (unrelated condition).

We tested the context availability and dual coding hypotheses within brain areas that showed effects of semantic priming (i.e. context) and areas that showed effects of imageability. Context availability theory predicts that the level of cortical activity should be modulated by the interaction between context and imageability, such that effects of semantic priming should be larger when the word pairs are low imageable than when they are high imageable. In contrast, dual coding theory predicts that cortical activity should not be modulated by the interaction between context and imageability.

Materials and Methods

Subjects

Ten right-handed undergraduate participants were paid \$10/h for participating in the 2 h study. All were native English speakers. Participants were informed of all the procedures and gave written consent as specified in a protocol approved by the University Institutional Review Board. Ten additional right-handed, native English speakers participated in a behavioral version of the study outside the scanner.

Stimuli

A stimulus list of 320 word pairs was constructed. Half of the word pairs consisted of high imageable words, and half of the pairs consisted of low imageable words. Half of the word pairs in the word list were related in meaning, and half were unrelated. The criteria for selecting words from established norms and the results of pre-test ratings have been described elsewhere (Swaab *et al.*, 2002). Critically, the strength of the relationship between related word pairs did not differ across high and low imageability conditions, thereby ensuring equivalent contextual support for high and low imageable words.

Each word pair was presented only once during the entire experiment. Words were presented in white lower-case sans serif font (each letter subtended $-0.66^\circ \times 1.33^\circ$) on a gray frame background ($10^\circ \times 2^\circ$), centered on fixation. The rest of the screen was black. Stimuli were displayed with an LCD projector located in the scanner room that back projected onto a screen attached to the scanning bed.

Procedure

Each trial consisted of the sequential presentation of the word pairs at fixation (duration = 300 ms), separated by a 500 ms interstimulus interval during which on a fixation cross was on the screen. Each trial was separated by an 8900 ms intertrial interval, during which subjects gave their response. The subject's task was to maintain fixation, read the words and indicate with a right-handed button press, as accurately as possible with no emphasis on speed, whether the word pairs were related or unrelated. Word pair relatedness and imageability were combined factorially and randomly intermixed in each run. There

were a total of 80 trials in each condition that were separated into eight experimental blocks.

Imaging

Functional images were acquired with a General Electric 1.5 T scanner equipped with an Advanced Development Workstation for real-time echoplanar imaging. Images were acquired using a T_2^* -weighted gradient-echo, echo-planar imaging sequence with a repetition time (T_R) of 2.0 s, echo time (T_E) 40 ms, and a flip angle (FA) of 90° . Twenty-four contiguous slices were collected with a voxel size of $3.75 \times 3.75 \times 5.0$ mm. Anatomical images were acquired using a T_1 -weighted sequence with a $T_R = 500$ ms, $T_E = 14$ ms, and FA of 90° and a voxel size of $0.94 \times 0.94 \times 5.0$ mm.

Image processing was performed using SPM99. Functional images were corrected for differences in slice acquisition order and motion. Two participants showed evidence of excessive head motion (>3 mm) during the scanning session and were therefore excluded from further analyses. Each of the remaining participants' anatomical scans were coregistered with their own functional images and then spatially normalized to stereotactic space using the Montreal Neurological Institute template. The resulting parameters were then used to spatially normalize the functional images. The normalized functional images were spatially smoothed with an 8 mm isotropic Gaussian kernel.

Statistical Analyses

Areas sensitive to semantic priming (i.e. context) were defined as those regions that were more activated on unrelated trials than on related trials; and areas sensitive to imageability were defined as those areas that were more active on high imageable trials than on low imageable trials. Regions that showed effects of context and imageability were identified in two steps. First, voxel-wise, fixed-effects *t*-tests of activity at the peak of the hemodynamic response (i.e. 4–6 s) were performed and the resulting maps were thresholded with a $P < 0.005$ (uncorrected) and an extent of 10 contiguous voxels. Second, to ensure that regions revealed in the first step were consistent across subjects a region of interest (ROI) analysis was performed where peak per cent signal change was calculated for each subject in each of the activated clusters. These values were then entered into a repeated measures ANOVA to test for main effects of context and imageability. Regions were considered to be significantly activated only if they survived the voxel-wise threshold at the first step and the region-wise threshold of $P < 0.05$ at the second step. We tested for the interaction between context and imageability within the regions revealed by the direct comparisons by computing the mean peak signal change for each subject in each condition, which were then entered into a repeated measures ANOVA.

Results

To distinguish between the predictions of the context availability theory and those of the dual coding theory it was determined whether cortical activity was modulated by the interaction between our manipulations of context and imageability. We tested for this interaction in two sets of regions: (i) areas that were modulated by semantic priming and (ii) areas that were modulated by imageability.

Semantic Priming Areas

Functional neuroimaging studies of repetition priming (Schacter and Buckner, 1998; Buckner *et al.*, 2000; Wagner *et al.*, 2000) and human electrophysiological studies of semantic priming (Swaab *et al.*, 2002) have demonstrated that areas that are involved in priming show more activity to unrelated or novel stimuli compared to related or repeated stimuli. Consistent with this literature, we identified those areas that showed more activity on unrelated trials than on related trials as areas that showed effects of semantic priming and were therefore sensitive to our manipulation of context. Several

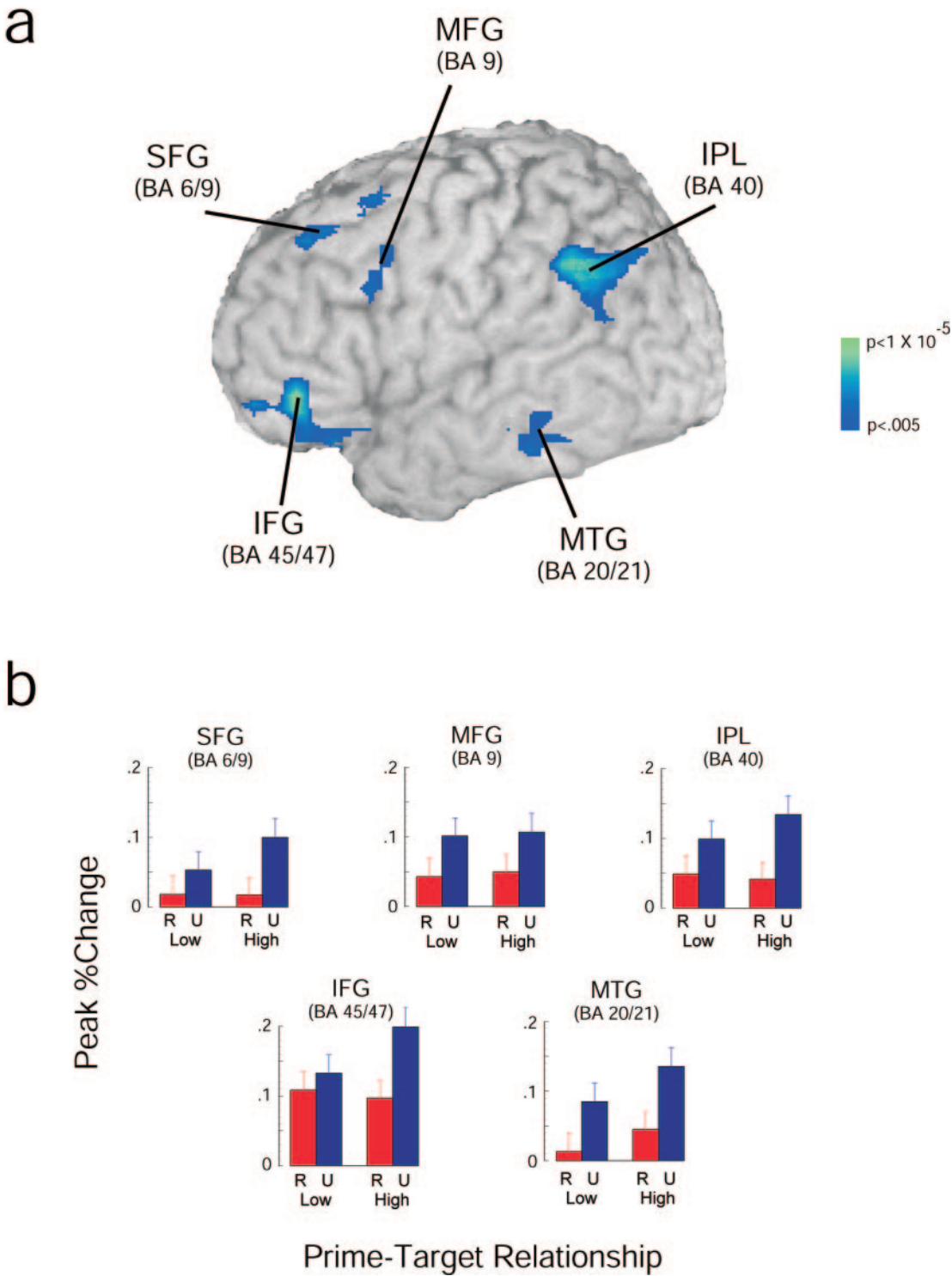


Figure 2. Results of context manipulation. (A) Areas that were significantly more active on unrelated than on related trials are overlaid onto a 3-D rendering of a single subject's high resolution anatomical image. These regions were significantly activated at the fixed and random effects levels (see Methods). Color bar represents P -value of fixed-effects analysis. See Table 1 for statistics for random effects analysis. (B) Averaged peak per cent signal change in each of the regions shown in A shown as a function of prime-target relationship, i.e. imageability (**High/Low**) and relatedness (**Related/Unrelated**). Error bars represent standard error of the mean. Abbreviations are as in Table 1.

areas showed significant effects of context (Fig. 2a and Table 1). Consistent with previous studies of semantic processing, these regions were isolated in the left hemisphere and included anterior portions of inferior frontal gyrus (IFG), roughly consistent with BA 45/47; dorsolateral prefrontal cortex, including

both middle and superior frontal gyri (MFG, BA 9; SFG, BA 6/9); inferior parietal cortex (IPL, BA 40), and middle temporal gyrus (MTG, BA 20/21).

Peak activity in each of the priming regions was calculated and is shown in Figure 2b. In addition to showing significantly

more activity on unrelated trials, two of these areas, IFG and SFG, showed significantly more activity to high imageable words than low imageable words (Figure 3 and Table 2). Critically, however, none of these areas exhibited significant interactions between context and imageability in terms of activity (see Table 1). Although not statistically significant, it is noteworthy that the trend of the interaction between context and imageability in IFG and SFG was in the direction of larger effects of context when the words were high imageable than when the words were low imageable, which is opposite to the prediction of the context availability hypothesis.

Imageability Areas

Areas that showed more activity on high imageable trials than low imageable trials are shown in Figure 3a and Table 2. As with the priming regions, areas that showed the imageability effect were isolated in the left hemisphere. These regions included anterior IFG (BA 45/47), posterior IFG extending to the precentral gyrus (PreCG; BA 44), left MTG (BA 20/21), and left medial frontal gyrus. Semantic priming also activated similar regions of IFG and MTG, but those areas that showed effects of imageability were more posterior and superior to the regions showing semantic priming. The anatomical separability between regions modulated by context and regions modulated by imageability is shown in Figure 4, where the activation maps in Figures 2 and 3 are overlaid on a single brain rendering.

Of the areas that showed more activity for high imageable words than for low imageable words only one, the medial frontal gyrus MedFG (BA 6/8), exhibited activity that was significantly modulated by the interaction between context and imageability (see Table 2). In addition, posterior IFG (BA 44) showed a marginal interaction between context and imageability ($P > 0.06$). However, activity in both MedFG and the

posterior portion of IFG showed larger priming effects on high imageable trials than on low imageable trials – again, in contrast to the context availability hypothesis.

Behavior

Overall mean accuracy during the behavioral session as a function of context and imageability is shown in Table 3. Participants showed the typical imageability and semantic priming effects, such that they were both more accurate on high imageable trials than on low imageable trials [91.6 vs 85.2% ; $F(1,9) = 30.87$; $P < 0.001$] and more accurate on related trials than on unrelated trials [93.3 vs 83.4% ; $F(1,9) = 7.14$; $P < 0.03$]. Consistent with the dual-coding hypothesis, there was no interaction between context and imageability ($F < 1$).

Discussion

The purpose of this study was to investigate the organization of semantic representations in the human brain. Specifically, we investigated whether separable brain regions are involved in the processing of verbal-based and image-based representations of words. To this end, we tested two competing hypotheses that make specific claims about how contextual information and imageability interact in word processing. The context availability hypothesis predicts that facilitated processing due to supporting context should be larger for low imageable words than for high imageable words. The dual coding hypothesis, on the other hand, predicts that supporting context should not modulate effects of imageability. We tested these hypotheses using event-related fMRI and a semantic priming paradigm where the contextual relationship and imageability of the prime and target words were manipulated. Two key aspects of our fMRI results support models such as the dual coding hypothesis, that posit the semantic system contains at least two types of representations, one based prima-

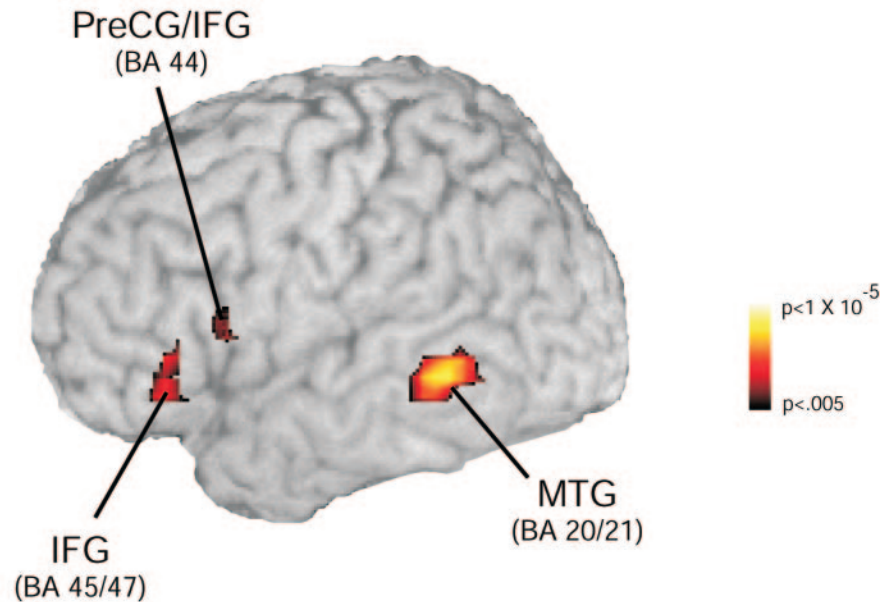
Table 1
Regions showing the effect of context (Unrelated > Related)

Region	Maxima	Coordinates (mm)			Voxel-wise main effect		Region-wise main effect		Context × Imageability interaction	
		x	y	z	T-value	P-value	F-value*	P-value	F-value	P-value
(-BA)										
Anterior lateral prefrontal (45/47)							12.67	<0.02	3.95	>0.08
	IFG	-52	28	-18	3.65	<0.0002				
	MFG	-41	43	-6	4.92	<0.0000005				
Temporal (20/21)							6.86	<0.04	<1	
	MTG	-67	-37	-7	2.87	<0.003				
	ITG	-59	-37	-15	3.30	<0.0005				
Parietal (40)							11.99	<0.02	1.02	>0.34
	IPL	-41	-53	39	4.76	<0.000002				
Dorsomedial prefrontal (6/9)							13.11	<0.01	3.27	>0.11
	SFG	-15	17	54	3.61	<0.0002				
	MedFG	-15	31	40	4.16	<0.00002				
Dorsolateral prefrontal (9)							17.23	<0.005	<1	
	MFG	-45	20	31	3.35	<0.0005				

*F-values are from a repeated measures ANOVA with 1,7 degrees of freedom for both main effect and interaction terms.

Abbreviations: BA, Brodmann Area; IFG, inferior frontal gyrus; MFG, middle frontal gyrus; MTG, middle temporal gyrus; ITG, inferior temporal gyrus; IPL, inferior parietal lobe; SFG, superior frontal gyrus; MedFG, medial frontal gyrus.

a



b

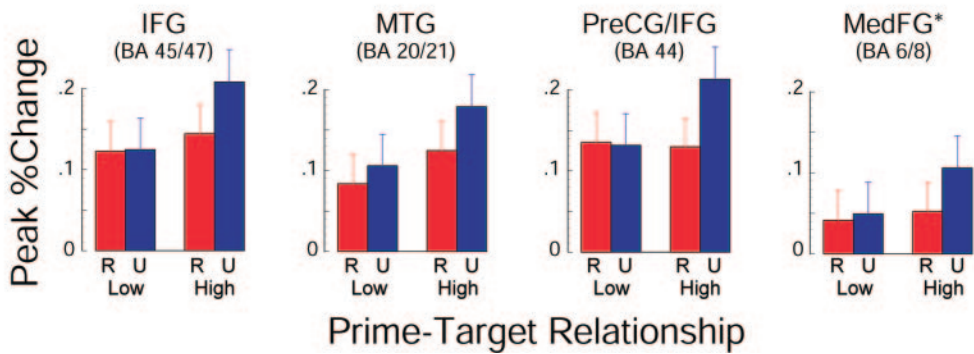


Figure 3. Results of imageability manipulation. (A) Areas that were significantly more active on high imageable than low imageable trials are overlaid onto a 3-D rendering of a single subject’s high resolution anatomical image. These regions were significantly activated at the fixed and random effects levels (see Methods). Color bar represents *P*-value of fixed-effects analysis. See Table 2 for statistics for random effects analysis. (B) Averaged peak per cent signal change in each of the regions shown in A shown as a function of prime–target relationship, i.e. imageability (**High/Low**) and relatedness (**Related/Unrelated**). *Activation not shown in Panel A. Error bars represent standard error of the mean. Abbreviations are as in Tables 1 and 2.

rily on verbal information and the other based primarily on perceptual information. We will discuss each in turn.

First, the most rigorous comparison of the context availability and dual coding hypotheses is in terms of whether cortical activity was modulated by the interaction between context and imageability. The test for this interaction was conducted in those areas that were modulated by context or imageability. In all but two of these regions, the pattern of brain activity indicated no interaction between context and imageability. This independence of contextual processing and imageability in terms of cortical activity provides strong support for the notion that the semantic system has access to

at least two kinds of representations. However, two areas showed indications of modulated activity as a function of the interaction between context and imageability. Although at first glance the presence of an interaction between context and imageability is more consistent with the context availability hypothesis than with the dual coding view, the interaction was driven by a larger effect of context for high imageable words than for low imageable words – opposite to what the context availability hypothesis predicts. How, then, is this interaction consistent with the dual coding view? According to a modified version of the dual coding hypothesis (Kounios and Holcomb, 1994; Holcomb *et al.*, 1999; West and Holcomb, 2000), larger

effects of context may occur for high imageable words when the selection of a contextual representation is difficult, and the semantic system has to rely on other semantic properties, such as imageability. Interestingly, one area that showed a trend towards this interaction, BA 44, is an area that has been implicated in the selection of semantic representations from task-relevant competing alternatives (Thompson-Schill *et al.*, 1997), also when this requires the selection of contextually appropriate meanings of ambiguous words (Swaab *et al.*, 1998). In the semantic judgment task used here, perhaps imageability enhanced the activation during poor supporting contexts, as may be the case when the prime and target were not related, in order to aid in task performance, thereby leading to a larger effect of context on high imageable trials than on low imageable trials. If this were true, then the observed interaction

should be found in other areas that are related to selection processes, including motor and/or response selection, and this was indeed the case. The other area to show this interaction was BA 6/8 on the medial surface on the left hemisphere, including the pre- and supplementary motor areas.

The second key aspect of our results was that areas that were sensitive to context were anatomically separable from those sensitive to imageability (Fig. 4). For instance, areas of parietal cortex (BA 40) and dorsal prefrontal cortex (BA 9/6) were modulated by context and not imageability, whereas, posterior inferior prefrontal cortex (BA 44) and medial frontal areas were modulated by imageability and not context. Thus, the activation of separable anatomical regions in our task might be taken as further evidence in favor of the dual coding hypothesis which posits that areas that process high imageable words should be independent of other contextual representations. It might be argued, however, that two key areas that have previously been shown to be involved in semantic processing, namely anterior portions of inferior prefrontal cortex (BA 45/47) (Thompson-Schill *et al.*, 1997; Poldrack *et al.*, 1999; Gold and Buckner, 2002) and middle temporal cortex (Martin and Chao, 2001; Gold and Buckner, 2002), were activated by both the manipulation of context and imageability. Indeed, the coactivation of these areas could be construed as inconsistent with the dual coding hypothesis. However, the anatomical locations of these activations did not precisely overlap: activations in the regions of BA 45/47 and BA 20/21 that were sensitive to our contextual manipulation were more anterior and inferior to activations in these same areas by the imageability manipulation. In sum, we have shown both functional and anatomical separability of effects of context and imageability, which supports the idea that semantic knowledge consists of multiple representational codes.

One question that may be raised with respect to the results of the present study is that, unlike in previous patient and ERP studies (Coltheart, 1980; Swaab *et al.*, 1996; Swaab *et al.*, 2002), we did not observe effects of imageability in the right hemisphere using our conservative two-step statistical analysis approach. Indeed, given the prior evidence in the literature, one would predict right hemisphere activity related to imageability. Therefore we returned to the data using less conservative fixed-effect analyses in order to investigate this further. These analyses revealed effects of imageability in the right

● Imageability Areas
● Context Areas

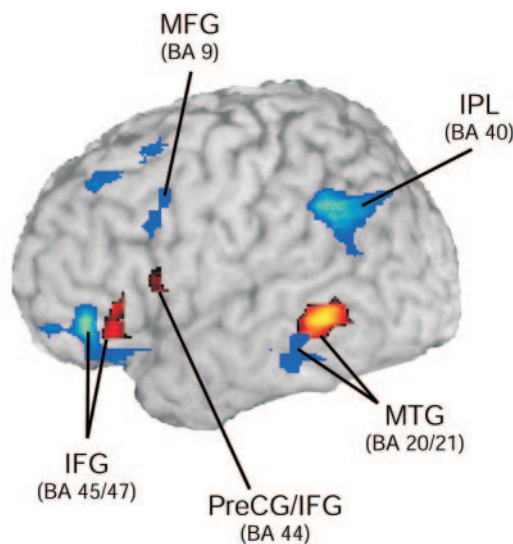


Figure 4. Combined results. Shown are the data from Figure 2 and Figure 3 overlaid onto a 3-D rendering of a single subject's high resolution anatomical image. Areas showing effects of priming/context are shown in blue and areas showing effects of imageability are shown in red. Abbreviations are as in Tables 1 and 2.

Table 2
Regions showing the effect of imageability (High > Low)

Region	Maxima	Coordinates (mm)			Voxel-wise main effect		Region-wise main effect		Context × Imageability interaction	
		x	y	z	T-value	P-value	F-value	P-value	F-value	P-value
(-BA)										
Anterior lateral prefrontal (45/47)	IFG	-56	33	3	3.85	<0.00007	10.1	<0.02	1.56	>0.25
Posterior lateral prefrontal (44)	PreCG/IFG	-48	15	8	3.15	<0.0009	8.65	<0.03	4.78	>0.06
Temporal (20/21)	MTG	-59	-51	3	4.55	<0.000003	11.97	<0.01	1.68	>0.23
Dorsomedial prefrontal (6)	MedFG	-4	38	35	2.91	<0.002	11.78	<0.02	6.18	<0.05

Abbreviations: PreCG, precentral gyrus; otherwise abbreviations are as in Table 1.

Table 3

Results of the behavioral session [per cent correct (standard error)]

Context	Imageability	
	Low	High
Related	90.5 (1.7)	96.1 (0.8)
Unrelated	79.8 (4.2)	87.0 (2.6)

hemisphere, including right MTG and SFG. This is consistent with previous studies, and also supports a dual coding view of semantic representations.

A second question that may be raised with respect to the results of the present study is that the related and unrelated trials differed in terms of context and they differed in terms of the response required (i.e. the word pairs were related or unrelated). Therefore it is possible that some, but not all, of what is attributed to context may also be due to differential decision processes. Although possible, there are several reasons why it is unlikely that differential decision processes are contaminating our results. Two are most critical. First, and perhaps most important, is that the effects of context in this paradigm do not depend on the type of response that is given. Previous studies have used no response or the same response as given here and found the same pattern of results (Swaab *et al.*, 1996, 2002). Second, because of the randomly intermingled conditions and the emphasis on accuracy, it would be in the participants' best interest to adopt a strategy that could be consistently applied across the trials. When considered together, these converging lines of evidence argue strongly that semantic priming effects observed here are not due to differential decision processes, but rather are due to differential supporting context.

In addition to providing evidence for separable semantic representations, the present results can also be brought to bear on neuroanatomical models of semantic processing. For instance a large body of literature has implicated anterior and posterior portions of left inferior prefrontal cortex as being critical in semantic processing (Thompson-Schill *et al.*, 1997, 1998, 1999; Schacter and Buckner, 1998; Poldrack *et al.*, 1999; Wagner *et al.*, 2000, 2001; Gold and Buckner, 2002). Anterior portions, near BA 45/47, are thought to be involved in the controlled retrieval of semantic information (Thompson-Schill *et al.*, 1997; Gold and Buckner, 2002). Posterior portions, near Broca's area (BA 44), are thought to be involved phonological processing (Poldrack *et al.*, 1999; Gold and Buckner, 2002) or selection of semantic information from competing alternatives (Thompson-Schill *et al.*, 1997). The activation of anterior prefrontal cortex in semantic priming, as we report here, is consistent with these models. When considered together with the greater activation of BA 45/47 and BA 44 (more activated to high imageable words than to low imageable words), the present results are more consistent with the notion that these areas are involved in the controlled retrieval of semantic and nonsemantic information (Gold and Buckner, 2002). Interestingly, however, the greater activity that we observed in BA 44 when high imageable words were presented in unrelated contexts is consistent with the view that under certain conditions BA 44 may be involved in the selection of semantic information from competing alternatives (Thompson-Schill *et al.*, 1997, 1998, 1999; Swaab *et al.*, 1998). Clearly, future research is needed to distinguish between these models of prefrontal

function in semantic processing, but the present results suggest that there may be a subdivision of labor within this area for processing semantic representations and the activation of these areas may depend on current processing demands.

Models of posterior cortical function in semantic processing suggest that as with BA 44, parietal cortex (BA 40), may be involved in processing phonological information (Gold and Buckner, 2002). Temporal cortex (BA 20/21), on the other hand, is sensitive to semantic processing, particularly categorical relationships (Chao *et al.*, 1999; Chao and Martin, 2000; Martin and Chao, 2001). Although the activation in parietal cortex observed here is consistent with the phonological processing account, it is also consistent with the other models of parietal function that suggest that it is involved in working memory and attentional operations, particularly the maintenance of task relevant representations (Wojculik and Kanwisher, 1999; Awh and Jonides, 2001). Thus, further research is required to understand how parietal and dorsal prefrontal brain circuits contribute during semantic processing. The activation of temporal cortex, on the other hand, particularly the dissociation of areas that responded to contextual information and imageability are entirely consistent with the current views of the role of this area in semantic and categorical processing. Indeed, several studies have demonstrated that there are subregions of temporal cortex that are sensitive to different types of categorical information (Chao *et al.*, 1999; Martin and Chao, 2001) and semantic information. Here we show that within the same task the contextual processing functions of temporal cortex are separable from the more posterior perceptual processing functions.

The present results demonstrate that cortical areas that are involved in semantic processing are not only anatomically separable, but more importantly these areas are highly sensitive to multiple sources of information that may be stored in different representational formats.

Notes

This research was supported by the McDonnell-Pew Program in Cognitive Neuroscience and the NIMH (B.G.) and the NSF (SES-0074 634 to T.Y.S.). We thank Jocelyn Sy for her help in collecting the behavioral data and Sean P. Fannon, Edith Kaan and George R. Mangun for their comments on earlier versions of this manuscript.

Address correspondence to Barry Giesbrecht, Center for Mind & Brain, University of California, One Shields Avenue, Davis, CA 95616, USA. Email: giesbrecht@ucdavis.edu.

References

- Awh E, Jonides J (2001) Overlapping mechanisms of attention and spatial working memory. *Trends Cogn Sci* 5:119-126.
- Barsalou LW (1991) Flexibility, structure, and linguistic vagary in concepts: manifestations of a compositional system of perceptual symbols. In: *Theories of memories* (Collins AF, Gathercole SE, Conway MA, Morris PE, eds), pp. 29-101. New York: Erlbaum.
- Barsalou LW, Simmons K, Barbey AK, Wilson CD (2003) Grounding conceptual knowledge in modality-specific systems. *Trends Cogn Sci* 7:84-91.
- Bentin S, McCarthy G, Wood CC (1985) Event-related potentials, lexical decision and semantic priming. *Electroencephalogr Clin Neurophysiol* 60:343-355.
- Buckner RL, Koustaal W (1998) Functional neuroimaging studies of encoding, priming, and explicit memory retrieval. *Proc Natl Acad Sci USA* 95:891-898.
- Buckner RL, Petersen SE, Ojemann JG, Miezin FM, Squire LR, Raichle ME (1995) Functional anatomical studies of explicit and implicit memory retrieval tasks. *J Neurosci* 15:12-29.

- Buckner RL, Koustaal W, Schacter DL, Rosen BR (2000) Functional MRI evidence for a role of frontal and inferior temporal cortex in amodal components of priming. *Brain* 123:620-640.
- Caramazza A, Hillis AE, Rapp BC, Romani C (1990) The multiple semantics hypothesis: multiple confusions? *Cogn Neuropsychol* 7:161-189.
- Caramazza A, Shelton JR (1998) Domain-specific knowledge systems in the brain: the animate-inanimate distinction. *J Cogn Neurosci* 10:1-34.
- Chao LL, Martin A (2000) Representation of manipulable man-made objects in the dorsal stream. *Neuroimage* 12:478-484.
- Chao LL, Haxby JV, Martin A (1999) Attribute-based neural substrates in temporal cortex for perceiving and knowing about objects. *Nat Neurosci* 2:913-919.
- Chao LL, Weisberg J, Martin A (2002) Experience-dependent modulation of category-related cortical activity. *Cereb Cortex* 12:545-551.
- Coltheart M (1980) Deep dyslexia: a right hemisphere hypothesis. In: *Deep dyslexia* (Coltheart M, Patterson KE, Marshall JC, eds), pp. 326-380. Boston, MA: Routledge & Kegan Paul.
- Dobbins IG, Foley H, Schacter DL, Wagner AD (2002) Executive control during episodic retrieval: multiple prefrontal processes subserved source memory. *Neuron* 35:989-986.
- Donaldson DI, Petersen SE, Buckner RL (2001) Dissociating memory retrieval processes using fMRI: evidence that priming does not support recognition memory. *Neuron* 31:1047-1059.
- Gold BT, Buckner RL (2002) Common prefrontal regions co-activate with dissociable posterior regions during controlled semantic and phonological tasks. *Neuron* 35:803-812.
- Goodglass H, Hyde MR, Blumstein SE (1969) Frequency, picturability and availability of nouns in aphasia. *Cortex* 5:104-119.
- Holcomb PJ (1993) Semantic priming and stimulus degradation: implications for the role of the N400 in language processing. *Psychophysiology* 30:47-61.
- Holcomb PJ, Neville HJ (1990) Auditory and visual semantic priming in lexical decision: a comparison using event-related brain potentials. *Lang Cogn Process* 5:281-312.
- Holcomb PJ, Kounios J, Anderson JE, West WC (1999) Dual-coding, context-availability, and concreteness effects in sentence comprehension: an electrophysiological investigation. *J Exp Psychol Learn Mem Cogn* 25:721-742.
- Jessen F, Heun R, Erb M, Granath D-O, Klose U, Papassotiropoulos A, Grodd W (2000) The concreteness effect: evidence for dual coding and context availability. *Brain Lang* 74:103-112.
- Kiehl KA, Liddle PF, Smith AM, Medrek A, Forster BB, Hare RD (1999) Neural pathways involved in the processing of concrete and abstract words. *Hum Brain Mapp* 7:225-233.
- Kieras D (1978) Beyond pictures and words: alternative information-processing models for imagery effects in verbal memory. *Psychol Bull* 85:532-554.
- Kounios, J and Holcomb, PJ (1994) Concreteness effects in semantic processing: ERP evidence supporting dual-coding theory. *J Exp Psychol Learn Mem Cogn* 20:804-823.
- Martin A, Chao LL (2001) Semantic memory and the brain: structure and processes. *Curr Opin Neurobiol* 11:194-201.
- Martin N (1996) Models of deep dyslexia. *Neurocase* 2:73-80.
- Meyer DE, Schvaneveldt RW, Ruddy MG (1975) Loci of contextual effects on visual word recognition. In: *Attention and performance V* (Rabbitt PMA, Dornic S, eds), pp. 98-118. New York: Academic Press.
- Miceli GRF, Capasso R, Shelton JR, Tomaiuolo F, Caramazza A (2001) The dissociation of color from form and function knowledge. *Nat Neurosci* 4:662-667.
- Neely JH (1977) Semantic priming and retrieval from lexical memory: roles of inhibitionless spreading activation and limited-capacity attention. *J Exp Psychol Gen* 106:226-254.
- Paivio A (1991) Dual coding theory: retrospect and current status. *Can J Psychol* 45:255-287.
- Petersen SE, Fox PT, Posner MI, Mintun M (1988) Positron emission tomographic studies of the cortical anatomy of single-word processing. *Nature* 331:585-589.
- Poldrack RA, Wagner AD, Prull MW, Desmond JE, Glover GH, Gabrieli JDE (1999) Functional specialization for semantic and phonological processing in the left inferior prefrontal cortex. *Neuroimage* 10:15-35.
- Richardson JT (1975) Concreteness and imageability. *Q J Exp Psychol* 27:235-249.
- Rossell SL, Price CJ, Nobre AC (2003) The anatomy and time course of semantic priming investigated by fMRI and ERPs. *Neuropsychologia* 41:550-564.
- Schacter DL, Buckner RL (1998) Priming and the brain. *Neuron* 20:185-195.
- Schwanenflugel PJ, Shoben EJ (1983) Differential context effects in the comprehension of abstract and concrete verbal materials. *J Exp Psychol Learn Mem Cogn* 9:82-102.
- Shallice T (1988) Specialization in the semantic system. *Cogn Neuropsychol* 5:133-142.
- Squire LR, Ojemann JG, Miezin FM, Petersen SE, Videen TO, Raichle ME (1992) Activation of the hippocampus in normal humans: a functional anatomical study of memory. *Proc Natl Acad Sci USA* 89:1837-1841.
- Swaab TY, Baynes K, Knight RT (1996) ERP evidence for the effect of imageability and semantic distance in word processing. *Psychophysiology*, 33, S81.
- Swaab TY, Brown C, Hagoort P (1998) Understanding ambiguous words in sentence contexts: electrophysiological evidence for delayed contextual selection in Broca's aphasia. *Neuropsychologia* 36:737-761.
- Swaab TY, Baynes K, Knight RT (2002) Separable effects of priming and imageability on word processing: an ERP study. *Cogn Brain Res* 15:99-103.
- Thompson-Schill SL, D'Esposito M, Aguirre GK, Farah MJ (1997) Role of left inferior prefrontal cortex in retrieval of semantic knowledge: a reevaluation. *Proc Natl Acad Sci USA* 94:14792-14797.
- Thompson-Schill SL, Swick D, Farah MJ, D'Esposito M, Kan IP, Knight RT (1998) Verb generation in patients with focal frontal lesions: a neuropsychological test of neuroimaging findings. *Proc Natl Acad Sci USA* 95:15855-15860.
- Thompson-Schill SL, D'Esposito M, Kan IP (1999) Effects of repetition and competition on activity in left prefrontal cortex during word generation. *Neuron* 23:513-522.
- Wagner AD, Koustaal W, Maril A, Schacter DL, Buckner RL (2000) Task-specific repetition priming in left inferior prefrontal cortex. *Cereb Cortex* 10:1176-1184.
- Wagner AD, Paré-Blagojev EJ, Clark J, Poldrack RA (2001) Recovering meaning: left prefrontal cortex guides controlled semantic retrieval. *Neuron* 31:329-338.
- Warrington EK (1975) The selective impairment of semantic memory. *Q J Exp Psychol* 27:635-657.
- Warrington EK, McCarthy R (1987) Categories of knowledge: further fractionations and an attempted integration. *Brain* 110:1273-1296.
- Warrington EK, Shallice T (1984) Category-specific semantic impairments. *Brain* 108:829-853.
- West WC, Holcomb PJ (2000) Imaginal, semantic, and surface-level processing of concrete and abstract words: an electrophysiological investigation. *J Cogn Neurosci* 12:1024-1037.
- Wojciulik E, Kanwisher N (1999) The generality of parietal involvement in visual attention. *Neuron* 23:747-764.