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Modulation of the semantic system by word imageability

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A prevailing neurobiological theory of semantic memory proposes that part of our knowledge about concrete, highly imageable concepts is stored in the form of sensory-motor representations. While this theory predicts differential activation of the semantic system by concrete and abstract words, previous functional imaging studies employing this contrast have provided relatively little supporting evidence. We acquired event-related functional magnetic resonance imaging (fMRI) data while participants performed a semantic similarity judgment task on a large number of concrete and abstract noun triads. Task difficulty was manipulated by varying the degree to which the words in the triad were similar in meaning. Concrete nouns, relative to abstract nouns, produced greater activation in a bilateral network of multimodal and heteromodal association areas, including ventral and medial temporal, posterior-inferior parietal, dorsal prefrontal, and posterior cingulate cortex. In contrast, abstract nouns produced greater activation almost exclusively in the left hemisphere in superior temporal and inferior frontal cortex. Increasing task difficulty modulated activation mainly in attention, working memory, and response monitoring systems, with almost no effect on areas that were modulated by imageability. These data provide critical support for the hypothesis that concrete, imageable concepts activate perceptually based representations not available to abstract concepts. In contrast, processing abstract concepts makes greater demands on left perisylvian phonological and lexical retrieval systems. The findings are compatible with dual coding theory and less consistent with single-code models of conceptual representation. The lack of overlap between imageability and task difficulty effects suggests that once the neural representation of a concept is activated, further maintenance and manipulation of that information in working memory does not further increase neural activation in the conceptual store. © 2005 Elsevier Inc. All rights reserved.

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Introduction

The neural representation of conceptual knowledge is a topic of central interest in cognitive neuroscience. Extensive research in this area has focused on the organization of knowledge about concrete entities, motivated by observations of concrete object category-related processing deficits in neurological patients (for reviews, see Capitani et al., 2003; Caramazza and Shelton, 1998; Devlin et al., 1998; Farah and McClelland, 1991; Forde and Humphreys, 1999; Gainotti et al., 1995; Humphreys and Forde, 2001; Tranel et al., 1997; Tyler et al., 2000). Many functional imaging studies in normal volunteers have also examined category-related effects on brain activity during processing of concrete concepts (for excellent reviews, see Bookheimer, 2002; Damasio et al., 2004; Devlin et al., 2002; Martin and Chao, 2001; Price and Friston, 2002; Thompson-Schill, 2003). While the results have varied considerably, many of these studies show activation of left posterior-lateral temporal cortex (particularly the posterior middle temporal gyrus) during processing of manipulable artifact concepts relative to natural categories such as animals and faces (Cappa et al., 1998; Chao et al., 1999; Damasio et al., 1996; Grossman et al., 2002; Martin et al., 1996; Moore and Price, 1999; Mummery et al., 1996; Perani et al., 1999b; Phillips et al., 2002). Conversely, processing animal concepts often produces greater activation in more ventral temporal or temporal-occipital regions, such as the fusiform and lingual gyri (Cappa et al., 1998; Chao et al., 1999; Damasio et al., 1996, 2004; Emmorey et al., 2003; Grossman et al., 2002; Martin et al., 1996; Moore and Price, 1999; Mummery et al., 1996; Perani et al., 1995, 1999b; Thompson-Schill et al., 1999a).

One interpretation of these category effects is that they reflect differences in the type of attribute knowledge accessed for different object categories (Farah and McClelland, 1991; Martin et al., 2000; Warrington and McCarthy, 1987). For example, living things tend to have many salient, defining visual features, making activation of the correct concept highly reliant on access to knowledge about visual attributes. Conversely, tools and many other artifact concepts are distinguished on the basis of their functions, which could be partly encoded in motor programs and knowledge of the characteristic motion of artifacts. Implicit in this account is the

Table 1 Review of the literature comparing concrete to abstract noun semantic processing

Study	Task contrast	Concrete > Abst	ract	Abstract > Conc	rete
		Region (BA)	<i>x</i> , <i>y</i> , <i>z</i>	Region (BA)	x, y, z
D'Esposito et al. (1997), <i>n</i> =7	Generate mental image to aurally presented CN vs. listen passively to AN	L. Fusiform L. Premotor L. Ant. Cing.	-33, -48, -18 -45, -3, 31 -7, -3, 42	R. SFG R. Precuneus	19, 50, 24 4, -74, 35
Mellet et al. (1998), <i>n</i> =8	Generate mental image to aurally presented CN definitions vs. listen passively to AN definitions	L. ITG/Fus.	-44, -58, -22 -42, -32, -18 52, -50, -14	L. STG R. MTG R. STG/STS	-60, -22, 12 58, 2, -18 54, -20, 6
		L. ITG L. Precent/MFS	-52, -62, -6 -40, 4, 34	1	52, -26, 18
		L. Inf. Par. Lob. L. Precent. g.	-28, 14, 30 -46, -38, 46 -42, -16, 38		
Kiehl et al. (1999), $n = 6$	Lexical decision (CN vs. AN blocks) ^a	L. Premotor	-36, 4, 60 -	R. STG	56, 11, 0
Perani et al. (1999a,b), <i>n</i> =14	Lexical decision (CN vs. AN blocks) ^a	_	_	L. IFG. (47) R. IFG (47) L. STG R. TP R. P-O (39/19)	-44, 14, -4 52, 20, -12 -58, 8, -16 42, 16, -36 40, -70, 36
				R. Ant. Cing. R. Amyg.	$\begin{array}{c} 6, \ 16, \ 40\\ 30, \ -4, \ -8 \end{array}$
Jessen et al. (2000), <i>n</i> = 14	Encode CN vs. encode AN	L. Par. Lob R. Par. Lob L. Prefrontal L. Precuneus	-39, -69, 36 42, -63, 42 -42, 42, 9 -3, -57, 45	L. IFG R. Occipital g.	-57, 30, 3 33, -78, 12
Wise et al. (2000), <i>n</i> =18	Reading, hearing, and making semantic similarity judgments on words varying in imageability	L. Mid Fus.	-31, -40, -18 -35, -50, -14	L. STG	not reported
Grossman et al. (2002), <i>n</i> =16	"Pleasant" or "not pleasant" decision on printed names of animals, implements, and abstract nouns	_	-	[Abs > Implem] L. Post. Lat. TL [Abs > Anim]	-60, -32, 12
				L. Post. Lat. 1L L. Prefrontal R. Med Frontal R. Post. Lat TL	-52, -68, 4 -24, 44, 12 16, 36, -4 56, -32, 16
Fiebach and Friederici (2003), $n = 12$ Noppeney and Price (2004), $n = 15$	Lexical decision (CN vs. AN) Semantic relatedness decisions on CN and AN word triads	L. Basal TL –	-27, -41, 4 -	L. IFG L. IFG L. Ant. TP	-46, 23, 7 -54, 21, -6 -51, 18, -27 51, 0, 24
Binder et al. (in press) $n = 24$	Lexical decision (CN vs. AN)	I Angular g	-37 -74 26	L. MTG/STS L. IFG	-51, 9, -24 -60, -42, -6 -46, 18, -4
Diricer et al. (in press), n 24		R. Angular g.	52, -58, 22 54, -48, 33	2.110	-39, 15, 14 -35, 27, 7
		L. Post. Cing.	-12, -56, 11 -9, -45, 13	L. Precent	-48, 9, 25 -48, -7, 40
		R. Post. Cing.	-7, -37, 36 5, -35, 38	L. IFS	-48, 22, 17 -47, 33, 8
		L. Precuneus	-12, -62, 24 -3, -74, 31	L. SIG	-44, 12, -16 -54, 4, -9
		ix. 1 icculicus	11, -54, 35 3, -62, 41		
		L. MFG	-28, 25, 48 -38, 19, 42		
		R. MTG	49, -49, 14		

Amyg = amygdala; AN = abstract noun; Ant = anterior; Cing = cingulate; CN = concrete noun; Fus = fusiform; g = gyrus; IFG = inferior frontal gyrus; IFS = inferior frontal sulcus; ITG = inferior temporal gyrus; L = left; Lat = lateral; Lob = lobule; MFG = middle frontal gyrus; MTG = middle temporal gyrus; Par = parietal; P-O = parietal occipital; Post = posterior; Precent = precentral; R = right; STG = superior temporal gyrus; TL = temporal lobe; TPn = temporal pole.

^a These studies used a block design that combined activation from words and nonwords in each condition.

notion that conceptual knowledge is partially stored in perceptual and kinesthetic representations residing in or near the modalityspecific sensory-motor systems through which the concepts were originally learned. This idea has a long history in clinical neurology (Freud, 1891/1953; Wernicke, 1874) and has had considerable influence among modern theorists (e.g., Allport, 1985; Barsalou, 1999; Coltheart et al., 1998; Damasio, 1989; Geschwind, 1965; Glenberg and Robertson, 2000; Martin et al., 2000; Paivio, 1971; Pulvermüller, 1999).

Here we test the premise that conceptual knowledge about concrete objects is stored in sensory-based perceptual representations by assessing the effects of noun imageability on brain activation. Concrete nouns differ from abstract nouns in that the former refer to imageable concepts learned through sensory experiences, whereas abstract nouns are thought to derive their meaning largely from association with other words, most of which are also abstract. If concrete object concepts are partially stored as sensory-based perceptual knowledge, these codes should be activated by concrete nouns more than by abstract nouns. This theory was first fully articulated by Paivio as the dual coding theory (Paivio, 1971, 1986), which proposes that abstract concepts are encoded and stored in memory in the form of symbolic or "verbal" representations, whereas concrete concepts are dually encoded into memory as both verbal representations and "image" codes grounded in perceptual experience. From a neurobiological perspective, abstract nouns are hypothesized to rely on a verbal semantic system located in the language-dominant hemisphere, whereas concrete nouns access additional sensory-motor "image" codes located in both hemispheres.

Much previous research supports the idea that conceptual processes are modulated by word imageability. For example, individuals respond more quickly and more accurately when making lexical decisions about concrete nouns than abstract nouns (James, 1975; Kounios and Holcomb, 1994; Kroll and Merves, 1986), and concrete nouns are better recalled on memory tests than abstract nouns (Paivio, 1971, 1986). Neurological patients often show performance advantages for concrete over abstract nouns (Coltheart et al., 1980; Franklin et al., 1995; Goodglass et al., 1969; Katz and Goodglass, 1990; Roeltgen et al., 1983) or the converse (Breedin et al., 1995; Marshall et al., 1998; Warrington, 1975, 1981; Warrington and Shallice, 1984). Other supporting evidence comes from divided visual field studies that have shown a concreteness advantage for words presented to the right hemisphere (left visual field) but not the left hemisphere (Chiarello et al., 1987; Day, 1979; Deloche et al., 1987), studies of patients with corpus callosum injuries (Coltheart et al., 1980; Coslett and Monsul, 1994; Coslett and Saffran, 1989; Zaidel, 1978), and electrophysiological experiments (Holcomb et al., 1999; Kounios and Holcomb, 1994, 2000; Nittono et al., 2002), all of which suggest more extensive processing of concrete words than abstract words in the right hemisphere.

Despite such evidence, and despite the postulated theoretical difference in neural representation of imageable, concrete concepts and abstract concepts, functional neuroimaging studies on this topic have produced highly variable results (Table 1). Several studies, for example, showed no areas with greater activation for concrete relative to abstract words (Grossman et al., 2002; Kiehl et al., 1999; Noppeney and Price, 2004; Perani et al., 1999a; Tyler et al., 2001), and two others showed no

concreteness effects in the ventral temporal lobe where differences would be most expected (Binder et al., in press; Jessen et al., 2000). Two studies that did find an imageability effect in the temporal lobe were confounded by differences in the tasks (active imagery vs. passive listening) used in the concrete and abstract conditions (D'Esposito et al., 1997; Mellet et al., 1998), leaving only 2 studies out of 11 that clearly support the notion that the temporal lobe contains neural representations of perceptual knowledge (Fiebach and Friederici, 2003; Wise et al., 2000).

Another long-debated issue concerns hemispheric asymmetries in the processing of abstract and concrete concepts. As mentioned above, much behavioral and electrophysiological evidence supports the proposal, posited by dual coding theory, that concrete concepts are processed bilaterally, while abstract concepts are processed mainly in the language-dominant hemisphere. Most functional imaging studies, in contrast, suggest that concrete noun processing is strongly left lateralized. Only a few have shown right hemisphere areas with stronger responses to concrete words than abstract words (Binder et al., in press; Jessen et al., 2000; Mellet et al., 1998). Thus, a major prediction of the dual coding model, that the right hemisphere should be more strongly activated by concrete than abstract words, has garnered relatively little support to date. Results for abstract nouns have been somewhat more consistent. Several studies showed stronger activation for abstract nouns in the left superior temporal (Binder et al., in press; Kiehl et al., 1999; Mellet et al., 1998; Noppeney and Price, 2004; Perani et al., 1999a,b; Wise et al., 2000) and left inferior frontal regions (Binder et al., in press; Fiebach and Friederici, 2003; Jessen et al., 2000; Noppeney and Price, 2004; Perani et al., 1999a,b) compared to concrete nouns.

In the current fMRI study, we attempted to resolve some of these inconsistencies by using a larger sample of participants to ensure reliable activation patterns and by incorporating a task designed to ensure deep semantic processing. The activation task required participants to make semantic similarity judgments on a large number of concrete and abstract noun triads. In contrast to lexical decision - a task used in several previous studies, including one from our lab (Binder et al., in press) - semantic similarity judgment requires explicit access to semantic knowledge, which we hypothesized would more clearly reveal any differences between concrete and abstract noun processing. In addition, task difficulty was manipulated by varying the degree to which the words in the triad were similar or different in meaning. This manipulation allowed us to distinguish effects of task difficulty from effects of the concrete-abstract conceptual variable that was the focus of interest.

Methods

Participants

Twenty-eight adult, right-handed, native English speakers (19 women) were studied. Their mean age was 22.8 (SD=3.6; range=18 to 33) years, and their mean education was 15.1 (SD=1.8; range=12 to 18) years. Participants were excluded if they had a history of neurological disease, major psychiatric disturbance, substance abuse, or current psychoactive medication use. Informed consent was obtained from each participant prior to participation.

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Stimuli and activation tasks

The stimuli were visual word triads presented in a pyramid arrangement with a sample word (e.g., cheetah) positioned at the top center of the display and two choice words (e.g., tiger, wolf) on either side of the bottom of the display. Stimuli were projected onto an opaque screen mounted near the participant's feet. Participants viewed the screen in a darkened room through prism glasses and, if necessary, corrective lenses. Stimuli were presented in white on a black background.

Triads were composed of either concrete nouns or abstract nouns. Participants were instructed to select the choice word that was most similar in meaning to the sample. Concrete nouns were sampled from a wide variety of semantic categories, including animals (i.e., land animals, birds, sea creatures, insects), fruits and vegetables, carpentry tools, vehicles, musical instruments, furniture, and articles of clothing. Within a given triad, however, all concrete nouns were from the same semantic category.

Task difficulty was manipulated by varying the degree to which the choice words were similar in meaning to the sample. This manipulation was based on normative data collected from a large group (n=99) of undergraduates in a pilot study (Sabsevitz, unpublished). In the pilot study, participants were given a packet with a large number of concrete and abstract noun word triads (i.e., sample: choice 1-choice 2) and asked to rate how similar each choice word was to the sample in meaning, thus providing two ratings for each triad. A 10-point visual analog scale was used with the following labels: 1 or 2=not related; 3 or 4=low related; 5 or 6=somewhat related; 7 or 8=related; 9 or 10 = highly related. For each noun triad, a semantic similarity difference (SSD) score was computed by calculating the absolute difference between the ratings for the sample and each choice word; that is, abs [(sample: choice 1)-(sample: choice 2)]. The absolute SSD scores ranged from 0, reflecting no difference in the degree of similarity between the choices and the sample, to 9, reflecting a large difference in similarity between the choices and the sample. Based on the distribution of the absolute SSD scores, cutoff scores were used to form the easy and hard semantic trials. Easy trials had median SSD scores ranging from 4 to 8 (mean=5.85, SD=0.89) while hard trials had median SSD scores ranging from 0 to 3 (mean=1.53, SD=0.62).

A total of 120 concrete noun (60 easy, 60 hard) and 120 abstract noun (60 easy, 60 hard) trials were created for the fMRI study. The concrete and abstract noun conditions were matched for letter length (overall mean=5.58, F(3,239)=0.205, P>0.05). There was also no difference in letter length between the easy and hard trials. Imageability ratings were obtained from the MRC lexical database (Wilson, 1988) (online at www.psy.uwa.edu.au/ mrcdatabasewa_mrc.htm) and from compatible norms published by Bird and colleagues (2001) and Cortese and Fugett (2004). Imageability ratings were available for 623 of the 720 words. The experimenters judged the imageability of the remainder of the words. As expected, nouns used in the concrete condition had significantly higher imageability ratings (mean=594, SD=42) than the nouns used in the abstract condition (mean=420, SD=69; t (1,621)=37.73, P < 0.001). There were no differences in imageability between easy and hard trials. Examples of stimulus triads are shown in Appendix A.

Interleaved with the semantic task was a low-level visual-perceptual task, which required participants to match triads of

foreign character strings on font size. Results from this task are not a focus of the present study and will be described in a subsequent report.

Stimuli were presented using E-Prime software (Psychology Software Tools, Inc.; Pittsburgh, PA). A nonferrous response box was placed beneath the participant's left hand to record response data and reaction time. Responses were made by pressing either the left or right button on the response box corresponding to the location of the choices on the screen. The location of the correct (target) choice was randomly varied and counterbalanced across trials. Participants received instructions and brief practice with each task before entering the scanner. Instructions were also repeated prior to each imaging run.

FMRI image acquisition

Scanning was conducted on a commercial 1.5-T General Electric Signa scanner (General Electric Medical Systems, Milwaukee) using a three-axis local gradient coil optimized for whole-brain echoplanar imaging. High-resolution T1-weighted anatomical reference images were collected using a 3D spoiledgradient-echo sequence (SPGR, GE Medical Systems, Milwaukee) with the following parameters: echo time=5 ms, repetition time=24 ms, flip angle= 40° , excitations=1, slice thickness=1.2 mm, FOV=24 cm, matrix= $265 \times 192 \times 124$. Functional imaging employed a gradient-echo echoplanar sequence with the following parameters: echo time=40 ms, repetition time=2000 ms, FOV=24 cm, matrix = $64 \times 64 \times 21$ mm. Twenty-one contiguous sagittal slices, measuring 6 or 6.5 mm in thickness, covered the whole brain (voxel size = $3.75 \times 3.75 \times 6-6.5$ mm). Each functional series began with 4 baseline images (8 s) to allow for equilibrium of the magnetic resonance signal and ended with 2 images with variable echo time used in the reconstruction of the data.

Six functional imaging runs were collected. Each run produced 240 image volumes and lasted 8 min, for a total of 1440 image volumes. Each run included an equal number (n=10) of concrete easy, concrete hard, abstract easy, and abstract hard trials that were randomly ordered and intermixed with 40 visual-perceptual trials.

For each condition, stimuli were presented on the screen for 4000 ms and were followed by either a 2-, 4-, or 6-s interstimulus interval in which a crosshair was displayed in the center of the screen for visual fixation. An equal number of stimuli from each condition were followed by each interstimulus interval. The interstimulus interval was randomly varied to reduce multicollinearity between event types and thereby improve estimation of the condition-specific hemodynamic responses.

Image analyses

Image analyses were performed using the AFNI software package (Cox, 1996) (online at http://afni.nimh.nih.gov/afni). All functional volumes were registered to the first steady state (i.e., 5th) volume using an iterative, linear least squares method to reduce motion artifacts. Each time series was visually inspected for residual artifacts, and volumes with major artifacts were censored from the analyses. The individual runs were concatenated to produce one time series. A deconvolution analysis was performed to estimate the magnitude, variance, and temporal properties of the hemodynamic response at each voxel for each stimulus condition. Trials on which errors occurred were coded as a separate condition and not included in subsequent analyses. The magnitude of the

Table 2Reaction time data for the different conditions

Condition	Difficulty level	Percent accuracy (SD)	Reaction time (SD)
Concrete noun	Easy	99.0 (1.5)	1919.9 (173.1)
	Hard	88.1 (5.1)	2319.3 (225.0)
	Overall	93.6 (6.7)	2119.6 (283.2)
Abstract noun	Easy	98.5 (2.1)	1982.9 (169.7)
	Hard	85.7 (6.3)	2287.3 (243.2)
	Overall	92.1 (8.0)	2135.1 (258.8)

response was estimated from the time points between 4 and 8 s after the onset of the stimulus; this corresponded to the peak of the hemodynamic response and immediately surrounding time points.

Anatomical images and individual hemodynamic response magnitude maps for each condition were transformed into standard stereotaxic space (Talairach and Tournoux, 1988) with linear interpolation to 1 mm³ voxels. To compensate for residual variation in anatomy across participants, the unthresholded, stereotaxically resampled maps were spatially smoothed using a 5-mm full width at half maximum Gaussian filter. Randomeffects ANOVA, using the individual magnitude maps from each condition, assessed activation differences between task conditions. Monte Carlo simulation was used to estimate the overall significance level, or the probability of a false detection, for the entire data set. Based on the output from 5000 simulations using an individual voxel detection probability of P=0.001 and a cluster connection radius corresponding to the nearest neighbor, a minimum cluster size threshold of 236 voxels was chosen to provide a whole-brain corrected significance level of alpha = 0.05.

Results

Task performance

Performance was generally good across all conditions. Accuracy data and reaction time (RT) data for correct trials only are presented in Table 2. Two separate 2 (imageability: concrete noun, abstract noun) $\times 2$ (difficulty: easy, hard) ANOVA's were performed to examine differences in accuracy and RT across conditions. These analyses showed no main effect of imageability on either accuracy (F(1,236)=1.60, P=0.207) or RT (F(1,236)=0.34, P=0.559). However, the main effect for task difficulty was significant for both accuracy (F(1,236) =105.94, P < 0.0001) and RT (F(1,236) = 176.27, P < 0.0001), with participants making more errors and taking longer to make semantic decisions when the degree of similarity between words was more equal. There was no interaction between condition and task difficulty for either accuracy (F(1,236)=0.64, P=0.425) or RT (F(1,236)=3.22, P=0.074). A strong correlation (r=-0.70)was found between the SSD ratings obtained from the behavioral pilot study and RT data from the fMRI study.

FMRI results

Concrete-abstract comparison

A direct comparison between the concrete and abstract conditions showed potent effects of word imageability in several cortical regions. As shown in Fig. 1 and Table 3, the concrete condition produced stronger activation in several posterior parietal, ventral temporal, and dorsal prefrontal areas. In the frontal lobe, greater activation was observed bilaterally in the medial superior



Fig. 1. FMRI activation map for the concrete – abstract comparison. The data are presented as sequential left hemisphere (top) and right hemisphere (bottom) 6mm sagittal sections, with the stereotaxic x-axis coordinate (L/R) given for each section. Uncorrected voxel-wise probability values are coded using the color scale shown at the bottom. Areas showing greater activation in the concrete condition are shown in red-orange-yellow, and areas with greater activation in the abstract condition are shown in blue-cyan.

Table 3												
Stereotaxic	coordinate	locations	of activ	vation	peaks	for th	e contrast	between	concrete a	and abstra	ct nouns	

Concrete > Abstract					Abstract > Concrete				
Structure	x	у	Ζ	Z score	Structure	x	у	Ζ	Z score
Temporal Regions					Temporal Regions				
L. parahippocampal g.	-27	-22	-20	5.84	L. sup. temporal g.	-49	6	-14	4.80
	-25	-37	-12	5.02	L. sup. temporal s.	-46	-29	-3	4.22
L. inf. temporal g.	-57	-49	-14	4.34		-63	-51	12	3.25
L. fusiform g.	-45	-52	-15	3.85	L. mid. temporal g.	-59	-47	3	4.43
R. hippocampus/amygdala	21	-5	-14	4.93	R. sup. temporal g./s.	46	9	-17	3.69
R. hippocampus	25	-14	-18	4.01		47	-13	-9	3.62
R. parahippocampal g.	26	-26	-16	3.99		47	-1	-16	3.33
Parietal Regions					Frontal Regions				
L. angular/sup. occipital g.	-28	-79	36	4.76	L. inf. fontal g.	-43	22	-5	4.75
	-31	-66	31	4.15	-	-50	15	9	4.67
	-38	-73	41	3.69	L. sup. frontal g.	-9	49	33	4.29
R. angular g.	36	-60	32	4.50					
0 0	42	-69	31	4.25					
R. angular/supramarginal g.	45	-47	42	3.72					
Frontal Regions									
L. inf./orbital frontal g.	-22	26	-9	4.08					
L. inf./mid. frontal g.	-42	39	12	3.85					
L. mid. frontal g.	-37	27	19	4.16					
L. sup. frontal g.	-19	8	52	4.31					
L. subcallosal g.	-11	18	-12	3.62					
R. inf./orbital frontal g.	27	26	-7	4.62					
e	37	35	-8	3.78					
R. mid. frontal g.	28	10	46	5.12					
6	45	31	14	4.45					
	43	45	6	3.67					
Posterior Cingulate Region									
L. post. cingulate/isthmus	-14	-54	15	4.04					
R. post. cingulate/isthmus	6	-52	9	4.73					
1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	1	-62	26	3.77					
		-	-						

g = gyrus; inf = inferior; L = left; mid = middle; post = posterior; R = right; s = sulcus; sup = superior.

frontal gyrus, posterior middle frontal gyrus (BA 6/8), and orbital frontal cortex (BA 11/47). Stronger activation for concrete nouns was also found in the right inferior frontal gyrus (BA 45) and the left inferior frontal sulcus (BA 45/46). A major focus of greater activation for concrete nouns was centered on the collateral sulcus in the ventral inferior temporal cortex. This activation was more extensive in the left hemisphere and included the anteriormedial fusiform gyrus, parahippocampal gyrus, and anterior hippocampus. Stronger activation for concrete nouns was observed in the inferior parietal-occipital region in both hemispheres, involving the angular (BA 39) and superior occipital (BA 19) gyri. Finally, greater activation for concrete nouns was found posterior to the splenium of the corpus callosum. This focus spread across both hemispheres and included a portion of the posterior cingulate gyrus, cingulate isthmus, and ventral precuneus.

Abstract-concrete comparison

In contrast to the bilateral activation associated with the concrete noun condition, processing abstract nouns produced greater activation primarily in left-lateralized areas (Fig. 1, Table 3). A large portion of the left inferior frontal gyrus, including the pars opercularis, pars triangularis, and pars orbitalis (BA 44, 45, 47), was activated more by abstract than by concrete nouns. Stronger activation by abstract nouns was also observed in the anterior left superior temporal gyrus and along the entire length

of the left superior temporal sulcus in the temporal lobe, spreading into the posterior dorsal middle temporal gyrus. A much smaller area of activation was found in the right superior temporal sulcus. The abstract noun condition also produced greater activation in the left medial superior frontal gyrus in an area corresponding to BA 9. This activation was anterior and medial to the superior frontal region of activation associated with the concrete noun condition.

Effect of increasing task difficulty

Irrespective of imageability, harder trials produced greater activation bilaterally along the cingulate sulcus, involving the cingulate and paracingulate gyrus and a portion of the medial superior frontal gyrus, as well as more dorsal aspects of the left inferior frontal gyrus and left inferior frontal sulcus (BA 44, 45, and 46) and more superior aspects of the precentral sulcus (BA 6 and frontal eye field). The right inferior frontal gyrus (dorsal BA 44 near the inferior frontal sulcus) was activated to a lesser degree. Increasing task difficulty also produced greater activation bilaterally in the anterior insula (right>left) and several deep brain structures, such as the midbrain, anterior thalamus, and lentiform nucleus (Fig. 2). A small region of increased activation was also found in the left superior parietal lobule at the anterior aspect of the intraparietal sulcus. As shown in the composite map of Fig. 3, overlap between the regions modulated by the concreteness and task difficulty factors was minimal. The only



Fig. 2. FMRI activation map for the main effect of task difficulty, collapsed across noun class. The data are formatted as in Fig. 1.

regions of significant overlap were in the pars triangularis of the inferior frontal cortex (BA 45) and in a small portion of the parietal lobe at the anterior edge of the region identified in the concrete–abstract comparison.

Discussion

Concrete, highly imageable nouns produced greater activation than abstract nouns in a bilateral network of multimodal and



Fig. 3. Composite map showing overlap between areas modulated by the imageability and task difficulty factors. The data are formatted as in Fig. 1. Areas of greater activation for concrete than abstract nouns are shown in blue, areas with greater activation for abstract than concrete nouns are shown in yellow, areas showing activation in response to task difficulty are shown in red, and any overlapping areas are shown in green.

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heteromodal association areas, including ventral temporal, posterior parietal, dorsal and dorsolateral prefrontal, and posterior cingulate cortex. This modulation of neural activity is unlikely to have been caused by differences in general attentional, working memory, selection, or decision demands. There were no significant differences in RT or accuracy between these conditions, and error trials were removed from the analysis. Moreover, a strong manipulation of task difficulty, produced by varying the degree of semantic similarity between sample and choice items, had no effect on activation in most of these regions. These results suggest that concrete concepts activate a more extensive representation in semantic memory than abstract concepts. Because abstract concepts – by definition – lack salient sensory–motor attributes, these data are consistent with the claim that concrete concepts are partly represented by knowledge about such attributes.

Sensory-motor representations in semantic memory

Evidence that concrete concepts are partly represented as modality-specific sensory-motor knowledge comes from prior empirical observations of neurological patients with semantic impairments (e.g., Buxbaum and Saffran, 1998; Coltheart et al., 1998; Sartori and Job, 1988; Silveri and Gainotti, 1988; Sirigu et al., 1991; Warrington and McCarthy, 1987; Warrington and Shallice, 1984; though see Caramazza and Shelton, 1998; Caramazza et al., 1990; Forde et al., 1997; Lambon Ralph et al., 1998) and from a number of functional imaging studies (e.g., Cappa et al., 1998; Chao and Martin, 1999; James and Gauthier, 2003; Kable et al., 2002; Kan et al., 2003; Kellenbach et al., 2001; Martin et al., 1995; Mummery et al., 1998; Phillips et al., 2002; Thompson-Schill et al., 1999a). While differences in neural activation for concrete and abstract nouns would seem to be a prerequisite for such a claim, previous results from studies using this contrast have provided relatively little support (Table 1). There are several possible explanations for these inconsistent findings. Of the five studies that failed to find greater activation for concrete noun processing in any brain regions, three (Kiehl et al., 1999; Perani et al., 1999a,b; Tyler et al., 2001) were lexical decision studies using a block design that combined the activation from words and nonwords in each condition. Because the nonword responses presumably did not differ between conditions, the contribution from the nonword trials may have masked differences in conceptual processing between the concrete and abstract words. A fourth study (Noppeney and Price, 2004) included a large number of stimuli in the concrete condition that were of questionable imageability (e.g., pop, transparent, music, picking). Furthermore, all of these studies used relatively small sample sizes (6 to 16 participants) compared to the present study, which may have limited detection of small but reliable activation effects.

The ventral visual pathway has been a particular focus of interest in testing the 'sensory-motor hypothesis' of conceptual representation. As mentioned in the Introduction, many neuroimaging studies have shown activation in ventral occipital and temporal locations during processing of living things relative to other concepts (e.g., Cappa et al., 1998; Chao et al., 1999; Damasio et al., 1996, 2004; Emmorey et al., 2003; Grossman et al., 2002; Martin et al., 1996; Moore and Price, 1999; Mummery et al., 1996; Perani et al., 1995, 1999b; Thompson-Schill et al., 1999a). The ventral position of these activations has usually been interpreted in modality-specific terms as related to the salient visual properties of animals and other living things. Several other studies have shown activation along the ventral visual pathway during retrieval of specific visual attribute knowledge (Chao and Martin, 1999; Kan et al., 2003; Kellenbach et al., 2001; Martin et al., 1995; Mummery et al., 1998; Thompson-Schill et al., 1999a) and during explicit mental imagery tasks (D'Esposito et al., 1997; Howard et al., 1998; Ishai et al., 2000; Kosslyn and Thompson, 2000; Mellet et al., 1998; O'Craven and Kanwisher, 2000).

Several prior studies contrasting concrete and abstract noun processing showed activation in the left fusiform gyrus for concrete items. In two of these studies, an explicit imagery task was used in the concrete condition and a passive listening task was used in the abstract condition, confounding the imageability factor with a task manipulation (D'Esposito et al., 1997; Mellet et al., 1998). Wise et al. (2000) observed a positive correlation between activation in the left mid-fusiform gyrus and word imageability during reading, listening, and semantic decision tasks. Fiebach and Friederici (2003) found activation in the left basal temporal lobe, very close to the site of activation seen by Wise et al., for concrete nouns relative to abstract nouns during an event-related lexical decision study. In contrast to these positive results, however, seven other studies comparing concrete and abstract words failed to show modulation of the ventral temporal lobe by word imageability (Binder et al., in press; Grossman et al., 2002; Jessen et al., 2000; Kiehl et al., 1999; Noppeney and Price, 2004; Perani et al., 1999a; Tyler et al., 2001).

The absence of temporal lobe effects in the study by Binder et al. (in press) is particularly notable. This study employed carefully controlled stimuli and a large subject sample and otherwise showed activation associated with word imageability in many of the same regions reported in the current study. We attribute the lack of temporal lobe activation in the prior study to use of a lexical decision task, which does not require explicit retrieval of perceptual knowledge. In contrast, the semantic similarity task used in the current experiment explicitly requires retrieval of attribute knowledge in order to judge similarity. The sensitivity of the fusiform gyrus and surrounding areas to word imageability during an explicit semantic task but not during lexical decision is reminiscent of a recent observation by Kan et al. (2003), who found activation of the left fusiform gyrus during a conceptproperty verification task (e.g., judge whether 'cake-frosting' is a correct pairing of a concept with a property) relative to a perceptual baseline task. Notably, this activation occurred only when the false trials contained highly associated words (e.g., 'stapler-paper'), thus necessitating explicit access to visual property knowledge for correct task performance, and not when the false trials contained unassociated words that could be rejected using an associative strategy. The robust modulation of this region by word imageability in the current study provides strong additional evidence that explicit retrieval of knowledge about imageable concepts involves modality-specific, visual association cortex.

Hemispheric asymmetries in processing concrete and abstract concepts

A second issue addressed in the current study concerns hemispheric differences in the processing of concrete and abstract concepts. According to Paivio's (1971, 1986) dual coding theory, abstract concepts are stored in a verbal semantic system located in the language-dominant hemisphere, while concrete concepts are represented in a nonverbal 'image-based' semantic system located in both hemispheres. As noted in the Introduction, there is considerable neuropsychological and electrophysiological evidence supporting the idea that the nondominant hemisphere is more proficient at processing concrete, imageable words than abstract words (Chiarello et al., 1987; Coltheart et al., 1980; Coslett and Monsul, 1994; Coslett and Saffran, 1989; Day, 1979; Deloche et al., 1987; Holcomb et al., 1999; Kounios and Holcomb, 1994, 2000; Nittono et al., 2002; Zaidel, 1978). This model predicts that relative activation for concrete nouns over abstract nouns should occur in the right hemisphere on functional imaging studies, but this prediction has been born out in only a minority of such studies (Binder et al., in press; Jessen et al., 2000; Mellet et al., 1998). The present finding of greater activation for concrete nouns in several right hemisphere areas provides new support for this model. Right brain areas showing this effect, including the angular gyrus, ventral temporal cortex, and posterior cingulate gyrus, were similar to those reported previously (Table 1).

On the other hand, greater activation for concrete items was also observed in several left hemisphere regions, in agreement with previous concrete-abstract comparisons (Binder et al., in press; D'Esposito et al., 1997; Fiebach and Friederici, 2003; Jessen et al., 2000; Mellet et al., 1998; Wise et al., 2000). This semantic network includes the angular gyrus, dorsal prefrontal cortex in the middle and superior frontal gyri, left ventral temporal cortex, and left posterior cingulate gyrus. Smaller foci were observed in the dorsolateral prefrontal cortex (inferior frontal sulcus), orbital frontal cortex, and posterior inferior temporal gyrus. This set of brain regions is very similar to that reported in many previous studies in which participants made semantic decisions about concrete nouns relative to performing nonsemantic tasks (e.g., Binder et al., 1999; Démonet et al., 1992; Mummery et al., 1998; Price et al., 1997; Roskies et al., 2001; Scott et al., 2003; Vandenberghe et al., 1996). These regions were also shown in several event-related lexical decision studies to respond more strongly to words than to pseudowords, suggesting a role in lexical-semantic access (Binder et al., 2003, in press; Ischebeck et al., 2004). These results make it clear that concrete concepts activate the left hemisphere at least as much as the right hemisphere, concordant with the view that knowledge about perceptual attributes of concrete concepts is stored and processed bilaterally.

The current results are also consistent with the idea that abstract concepts are processed mainly in the left hemisphere. Abstract nouns produced stronger activation than concrete nouns in several left brain regions, most prominently the left inferior frontal gyrus and superior temporal sulcus. Very similar results have been observed in other studies that directly contrasted abstract with concrete nouns (Binder et al., in press; Fiebach and Friederici, 2003; Mellet et al., 1998; Noppeney and Price, 2004; Perani et al., 1999a; Wise et al., 2000). One interpretation of these data is that the greater activation of these perisylvian regions by abstract nouns reflects the greater role of the verbal semantic system in processing abstract concepts. Abstract nouns have less access to perceptually based representations and are therefore more dependent on word associations for retrieval of meaning. Processing abstract nouns for meaning would therefore be expected to activate the verbal semantic system to a greater degree than concrete nouns. Thus, the left inferior frontal and superior temporal regions activated by abstract nouns may represent components of the putative verbal semantic system. Complicating this interpretation somewhat is the fact that Binder et al. (in press) also observed greater activation of some of these regions for pseudowords compared to concrete words. They interpreted this pattern as indicating a role for these

areas in phonological working memory and lexical search processes rather than in conceptual processing per se. It was proposed that abstract words engage these processes to a greater degree during lexical decision because of the slower semantic access for these words.

We believe that both of these accounts are partially correct and apply to somewhat different brain regions. Areas activated by pseudowords relative to concrete words in the Binder et al. (in press) study included only the more posterior aspects of the frontal region and the most anterior aspects of the temporal region. These areas may well be activated by abstract words relative to concrete words because of the greater demands on phonological working memory and/or lexical retrieval processes for abstract words. More anterior and ventral regions of the inferior frontal gyrus, particularly the pars orbitalis (BA 47), and more posterior aspects of the superior temporal sulcus, were not activated by pseudowords in the previous study and may therefore represent components of a verbal semantic system engaged more by abstract than by concrete concepts.

The results present difficulties for single-code models of concrete and abstract word representation, such as context availability theory (Schwanenflugel, 1991; Schwanenflugel and Stowe, 1989), which argues that all concepts are represented in an amodal semantic system. According to this model, concrete nouns are processed more efficiently than abstract nouns because they have stronger and more extensive links to contextual information stored in semantic memory (i.e., a greater quantity of information available). This model predicts generally greater activation for concrete words over abstract words, but not the converse. The observation here of greater activation for abstract words in several large left hemisphere regions is therefore not consistent with a single-code account.

Effects of task difficulty

We incorporated a task difficulty manipulation in an attempt to distinguish effects of imageability from general effects of task difficulty, and to determine whether brain areas modulated by imageability would be affected by attentional and working memory load. Examination of the behavioral data supports the effectiveness of the difficulty manipulation, in that participants had much longer response latencies and were less accurate on hard than easy trials. Although one might predict more extensive activation of semantic codes during trials in which the choices were more similar in meaning, the fMRI results show little overlap between the regions modulated by the imageability and difficulty factors. This finding suggests that the activation of semantic codes in these putative semantic regions occurs in a relatively 'all or none' fashion. That is, once the semantic representation of a concept is activated, further maintenance and manipulation of that semantic information in working memory does not appreciably increase the level of neural activation in the semantic memory network. Activation related to the difficulty manipulation occurred primarily in regions associated with attention, phonological working memory, lexical retrieval, decision making, and response monitoring, and likely reflects the increased demands placed on these systems by the harder trials.

In agreement with the present findings, two other studies reported remarkably similar activation patterns in response to processing more difficult lexical-semantic trials. Using a task similar to the one used here, Noppeney and Price (2004) categorized trials as either easy or hard based on event-specific reaction times. They found greater activation in the anterior cingulate cortex, left anterior insula, left inferior frontal region, and midbrain structures during hard semantic trials relative to easy trials. Binder and colleagues (in press) showed strong positive correlations between reaction time and degree of activation in the anterior cingulate cortex, bilateral anterior insula, bilateral inferior frontal gyrus, and midbrain structures during a lexical decision task.

Previous electrophysiological and neuroimaging studies (e.g., Badgaiyan and Posner, 1998; Botvinick et al., 1999; Braver et al., 2001; Carter et al., 1998; Dehaene et al., 1994; Falkenstein et al., 1991; Gehring et al., 1993; Taylor et al., 1994; Ullsperger and von Cramon, 2001; van Veen and Carter, 2002) suggest that the anterior cingulate cortex plays an important role in regulating behavior through the online monitoring of task performance. We found more activation in this region during hard trials, which may reflect increased demands on response selection and monitoring. Activation in the anterior insula has been reported in several imaging studies to be correlated with task difficulty and response time (Adler et al., 2001; Binder et al., 2004; Braver et al., 2001; Menon et al., 2001; Taylor et al., 1994; Ullsperger and von Cramon, 2001). Greater activation was also found in the left and to a lesser extent right inferior frontal cortex. This region has been implicated in a variety of phonological, verbal working memory, and selection processes (e.g., Awh et al., 1996; Barde and Thompson-Schill, 2002; D'Esposito et al., 1999; Fiez, 1997; Paulesu et al., 1993; Thompson-Schill et al., 1999b). The greater activation in this region during harder trials may reflect the longer period of time in which phonological, lexical, and conceptual information were held in working memory while comparing the semantic features of the three words. Finally, we found greater activation in subcortical areas, including the thalamus, caudate, and internal capsule, with activation extending into mesencephalic and pontine regions, during harder trials. This activation may reflect involvement of the ascending reticular activating system in modulating levels of arousal during hard trials. Previous imaging studies have found greater activation in the thalamus and mesencephalic region in response to attentional alerting and orienting demands (for a review, see Sturm and Willmes, 2001).

Conclusions

While many neurobiological accounts of semantic memory posit involvement of perceptually based codes in the representation of concrete concepts, functional imaging studies comparing concrete and abstract word processing have provided relatively little support for this view. The results reported here clarify the effects of word imageability on neural activation, demonstrating that a distributed, bilateral semantic memory system responds more strongly to concrete than abstract words. These data confirm findings from a recent event-related lexical decision study that showed stronger activation for concrete than abstract words in a very similar bilateral network (Binder et al., in press). The present results also extend these previous findings by demonstrating robust modulation of the ventral temporal cortex by word imageability, as predicted by the sensory–motor theory of conceptual processing but observed in only a minority of previous studies of word imageability.

The data demonstrate a relative dissociation between this bilaterally organized network sensitive to concepts with sensory-

motor attributes and a left-lateralized system specialized for processing abstract words. This pattern is consistent with the relative hemispheric asymmetry claims proposed by dual coding theory. The dissociation is also consistent with reports of patients with greater impairments for concrete words than abstract words following bilateral or unilateral ventral temporal lesions (Breedin et al., 1995; Warrington, 1975, 1981; Warrington and Shallice, 1984) and with the often-described pattern of greater impairment on abstract words following unilateral left perisylvian damage (Coltheart et al., 1980; Franklin et al., 1995; Goodglass et al., 1969; Katz and Goodglass, 1990; Roeltgen et al., 1983).

Finally, the results illustrate two interesting phenomena related to attentional modulation of the semantic memory store. As proposed previously by Kan et al. (2003), modulation of the ventral visual association cortex during lexical-semantic tasks appears to depend on the depth of processing required for task performance. Tasks that can be performed without the need for explicit retrieval of semantic attributes, such as lexical decision, do not appreciably activate this region (Binder et al., in press). On the other hand, once this attribute knowledge was activated, even a large increase in response selection and working memory demands in the present study did not further increase activation of this or other regions involved in semantic access.

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Appendix A

Sample stimulus items (sample: choice1-choice2; correct choice is presented in italics)

Easy Concrete Noun Triads	Hard Concrete Noun Triads
cheetah: pelican-tiger	cherry: grape—banana
trumpet: clarinet-pencil	beetle: ladybug-cricket
vulture: gorilla-crow	mosquito: butterfly-bee
canary: octopus-pigeon	pen: marker-chalk
sponge: napkin-drill	eagle: robin-hawk
spider: ant-buffalo	lemon: orange-pear
chipmunk: squirrel—goldfish	seal: shark-dolphin
apron: tuxedo—bib	bus: taxi-car
necklace: ring-shirt	skirt: pants-shorts
knife: jar—fork	violin: piano—guitar
5 5	
Easy Abstract Noun Triads	Hard Abstract Noun Triads
Easy Abstract Noun Triads myth: sanity—tale	Hard Abstract Noun Triads bravery: courage—strength
<i>Easy Abstract Noun Triads</i> myth: sanity— <i>tale</i> prank: <i>trick</i> —vision	Hard Abstract Noun Triads bravery: courage—strength idea: thought—belief
<i>Easy Abstract Noun Triads</i> myth: sanity— <i>tale</i> prank: <i>trick</i> —vision news: <i>media</i> —prayer	Hard Abstract Noun Triads bravery: courage—strength idea: thought—belief peace: freedom—treaty
<i>Easy Abstract Noun Triads</i> myth: sanity— <i>tale</i> prank: <i>trick</i> —vision news: <i>media</i> —prayer job: <i>career</i> —crime	Hard Abstract Noun Triads bravery: courage—strength idea: thought—belief peace: freedom—treaty victory: success—battle
<i>Easy Abstract Noun Triads</i> myth: sanity— <i>tale</i> prank: <i>trick</i> —vision news: <i>media</i> —prayer job: <i>career</i> —crime comedy: lesson— <i>humor</i>	Hard Abstract Noun Triads bravery: courage—strength idea: thought—belief peace: freedom—treaty victory: success—battle concern: worry—fear
<i>Easy Abstract Noun Triads</i> myth: sanity— <i>tale</i> prank: <i>trick</i> —vision news: <i>media</i> —prayer job: <i>career</i> —crime comedy: lesson— <i>humor</i> quality: <i>value</i> —fault	Hard Abstract Noun Triads bravery: courage—strength idea: thought—belief peace: freedom—treaty victory: success—battle concern: worry—fear danger: injury—threat
<i>Easy Abstract Noun Triads</i> myth: sanity— <i>tale</i> prank: <i>trick</i> —vision news: <i>media</i> —prayer job: <i>career</i> —crime comedy: lesson— <i>humor</i> quality: <i>value</i> —fault shame: <i>disgrace</i> —symbol	Hard Abstract Noun Triads bravery: courage—strength idea: thought—belief peace: freedom—treaty victory: success—battle concern: worry—fear danger: injury—threat error: accident—mistake
<i>Easy Abstract Noun Triads</i> myth: sanity— <i>tale</i> prank: <i>trick</i> —vision news: <i>media</i> —prayer job: <i>career</i> —crime comedy: lesson— <i>humor</i> quality: <i>value</i> —fault shame: <i>disgrace</i> —symbol rule: agony— <i>law</i>	Hard Abstract Noun Triads bravery: courage—strength idea: thought—belief peace: freedom—treaty victory: success—battle concern: worry—fear danger: injury—threat error: accident—mistake fate: destiny—future
Easy Abstract Noun Triads myth: sanity—tale prank: trick—vision news: media—prayer job: career—crime comedy: lesson—humor quality: value—fault shame: disgrace—symbol rule: agony—law design: plan—rumor	Hard Abstract Noun Triads bravery: courage—strength idea: thought—belief peace: freedom—treaty victory: success—battle concern: worry—fear danger: injury—threat error: accident—mistake fate: destiny—future asset: profit—labor

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