Neural Representation of Verb Meaning: An fMRI Study

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Abstract: The neural basis for verb comprehension has proven elusive, in part because of the limited range of verb categories that have been assessed. In the present study, 16 healthy young adults were probed for the meaning associated with verbs of MOTION and verbs of COGNITION. We observed distinct patterns of activation for each verb subcategory: MOTION verbs are associated with recruitment of left ventral temporal-occipital cortex, bilateral prefrontal cortex and caudate, whereas COGNITION verbs are associated with left posterolateral temporal activation. These findings are consistent with the claim that the neural representations of verb subcategories are distinct. Although the “sensory-motor” hypothesis may play a role in explaining activation associated with MOTION verbs, the left posterolateral temporal distribution of cortical activation associated with COGNITION verbs cannot be easily explained by the “sensory-motor” hypothesis. We suggest that left posterolateral temporal activation supports aspects of lexical semantic processing concerned with the neural representation of propositional knowledge contributing to COGNITION verbs. *Hum. Brain Mapping* 15:124–134, 2002. © 2002 Wiley-Liss, Inc.

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INTRODUCTION

Words contain many features that contribute to their meaning. Most work investigates the role of sensory-motor feature knowledge in the neural representation of meaning for specific categories of nouns. In

the present study, we compare categories of verbs to evaluate category-specific effects in another major lexical category.

Philosophers and linguists have emphasized several features that contribute to knowledge of verb meaning. Verbs of MOTION (we use capitals to indicate a concept) such as “fall” represent observable events [Jackendoff, 1983; Miller and Johnson-Laird, 1976]. These events typically involve planning for actions that depend on implementation by the motor system. Moreover, these events occur in a dynamic spatial framework as they unfold over time. Verbs of MOTION thus have a rich and elaborate set of associated perceptual and motor features.

By comparison, COGNITION verbs such as “ponder” are relatively impoverished in their associated motor and perceptual features. Indeed, most theories of word meaning concerned with the distinction be-

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tween concrete and abstract words note that abstract words contain fewer associated sensory-motor features [Plaut and Shallice, 1993; Schwanenflugel, 1991; Schwanenflugel and Shoben, 1983], and it is this paucity that accounts for our acquisition of abstract words later in development [Gentner, 1982] and our access to these more slowly as adults [Kroll and Merves, 1986; Paivio, 1991], in comparison to concrete terms. Several brain-damaged patients are described with “reversal of the concreteness effect” [Breedin et al., 1995; Sirigu et al., 1991; Warrington, 1975; Warrington and Shallice, 1984], that is, these patients are more impaired in their comprehension of concrete words. Based on these observations, abstract words do not appear to differ from concrete words simply by having fewer sensory-motor features, because the comprehension of abstract words presumably would have suffered a proportional decline following any general degradation of sensory-motor feature knowledge. Instead, abstract words are likely to have some non-sensory-motor property that plays little role in concrete words, and is crucial for the mental representation and processing of abstract words. Hints about this come from developmental psycholinguistic studies suggesting that abstract words are acquired after exposure to sentences containing propositions with these terms [Landau et al., 1992; Landau and Jackendoff, 1993]. Some investigators emphasize that an elaborated set of semantic relations is particularly characteristic of the concepts underlying abstract words [Gentner, 1981; Jackendoff, 1990; Pinker, 1989]. Abstract words such as verbs of COGNITION thus may depend in larger part on processing an elaborate series of propositions that contribute importantly to their meaning.

Much work investigating the neural representation of category-specific word knowledge has focused on nouns. One prominent anatomically-based approach to categories of noun knowledge, the “sensory-motor” hypothesis, emphasizes that semantic feature knowledge is stored in the cortical processing stream that reflects the modality (e.g., visual or motor) most relevant to the semantic feature [Allport, 1985; Martin et al., 2000; Warrington et al., 1984]. Functional neuroimaging studies of healthy adults thus have observed recruitment of left lateral temporal cortex during the presentation of manufactured artifacts such as TOOLS [Cappa et al., 1998; Chao et al., 1999; Damasio et al., 1996; Martine et al., 1996; Mummery et al., 1998; Perani et al., 1995], presumably reflecting the visual motion features associated with artifact use [Bonda et al., 1996; de Jong et al., 1994; Kourtzi and Kanwisher, 2000; Patzwahl et al., 1996; Puce et al., 1998]. Some functional neuroimaging studies of healthy adults also

have noted activation of premotor and prefrontal cortical regions in association with artifacts such as TOOLS [Grabowski et al., 1998; Grafton et al., 1997; Martin et al., 1996; Perani et al., 1995], presumably reflecting the motor action planning and motor implementation involved in the use of a manufactured artifact [Decety et al., 1994; Jeannerod et al., 1995; Rizzolatti et al., 1996a,b].

Work with abstract nouns, by comparison, is much rarer [Beauregard et al., 1997; Grossman et al., in press; Kiehl et al., 1999]. These studies associate abstract words with recruitment of left posterolateral temporal and left prefrontal brain regions. Grossman et al. (in press) argued that the overlap in recruitment patterns across these abstract nouns and some concrete word categories with rich sensory-motor features such as TOOLS calls to question strong versions of the sensory-motor hypothesis. These brain areas may be concerned not only with the neural representation of sensory-motor features, but also with processing propositional knowledge.

There are many differences between verbs and nouns, however, which may limit generalization across these word categories. For example, the structure of the semantic network organizing verbs appears to be less deep hierarchically than for nouns [Miller and Fellbaum, 1991]. Verbs may depend on different configurations of sensory-motor features, such as less dependence on imageability, compared to nouns [Bird et al., 2000]. Conversely, verbs appear to be much richer in their sentence-related features, specifying associated thematic roles and other grammatical limitations that are relatively rudimentary in nouns [Jackendoff, 1983; Miller and Johnson-Laird, 1976; Gleitman, 1990]. MOTION verb knowledge typically maps onto a sentence framework that contains some combination of direct and indirect objects representing the features of an event (e.g., goal, instrument) as thematic roles in a thematic matrix, in other words, an action-oriented representation of who is doing what to whom [Baker, 1988; Fisher et al., 1991; Grimshaw, 1987]. COGNITION verb knowledge, by comparison, maps onto a sentence frame that typically includes a sentence complement suitable for a proposition rather than a thematic matrix (e.g., the underlined portion of the sentence “I believe that the cow jumps over the moon”). Differences such as these may explain in part the results of many investigations showing greater difficulty in brain-damaged patients’ verb comprehension and naming relative to comparable measures with nouns [Berndt et al., 1997; Daniele et al., 1994; Miceli et al., 1984; Rhee and Grossman, 2001; White-Devine et al., 1996].

Because of noun-verb differences such as these, we cannot easily generalize from studies of the neural representation of noun categories to the neural representation of verb meaning. Only a small number of investigations have examined categories of verb knowledge directly. The association between verb meaning and left inferior frontal cortex has featured prominently in the “verb generation” task used so often since the seminal work of Petersen et al. [1988]. Some work, however, has suggested that inferior frontal activation may have less to do with verb meaning per se than task-related processes such as the encoding and retrieval of cross-category word associations [Demb et al., 1995; Kapur et al., 1994; Thompson-Schill et al., 1997; Tulving et al., 1994]. More recent observations have also noted activation of left posterolateral temporal cortices during verb generation [Fiez et al., 1996; Warburton et al., 1996]. In a clever design eliciting action knowledge of object names and object pictures, verb production was associated with left inferior frontal and left posterolateral temporal recruitment [Martin et al., 1995]. More recently, Italian subjects were asked to make a lexical decision about printed words [Perani et al., 1999]. This study demonstrated recruitment of left middle and inferior frontal gyri as well as left posterolateral temporal cortex in association with verb stimuli, although the verb category was marked with a grammatical morpheme.

These activation findings for verbs have been interpreted to support the claim that the neural representation of verb knowledge is related to the left posterior temporal and prefrontal substrate of the associated sensory-motor features. This work, however, focuses almost exclusively on MOTION verbs that refer to observable events. The one study investigating differences in category-specific knowledge across two verb categories failed to find a category-specific effect [Perani et al., 1999]. In the present study, we re-examine the category-specific effect in two domains of verb knowledge. Specifically, we test the generalizeability of the “sensory-motor” account for the neural representation of word meaning by contrasting MOTION verbs with verbs of COGNITION: we examine recruitment patterns for activation of sensory-motor association cortices related to MOTION verbs, and assess the relationship between abstract words like COGNITION verbs with left posterolateral temporal cortex where verbal, propositional knowledge may be represented and processed.

MATERIALS AND METHODS

Subjects

We studied 16 right-handed native English-speakers who were students at the University of Pennsylvania. This includes nine females and seven males, with a mean age of 23.4 years (range 19–28 years) and a mean education of 16.0 years (range 14–18 years). These subjects participated in an informed consent procedure approved by the IRB at the University of Pennsylvania.

Materials

We presented blocks of printed words to subjects that included citation forms of MOTION verbs and COGNITION verbs. The words were either unambiguously verbs, or if not, a word’s frequency of occurrence as a verb was at least five times its frequency of occurrence as a noun, according to form class-sensitive frequency measures [Francis and Kucera, 1982]. The categories of verbs were matched for mean frequency [Francis and Kucera, 1982] (COGNITION = 16.1; MOTION = 13.8: $t(118) = 0.83$; NS). A cohort of 42 native English-speaking undergraduates assessed the words for familiarity: The meanings of all the words were known to all students, and all but 14 of the 120 words were judged to be highly familiar by over 90% of these students (one motion verb was judged familiar by only 90% of students, five cognition verbs and two motion verbs were judged familiar by only 86% of students, and three cognition verbs were judged familiar by only 83% of students).

Subjects were asked to judge the “pleasantness” of each stimulus. We chose this single probe for all words to avoid explicit categorization of verb subcategories, where the content of the word category can influence the nature of the categorization process and thus confound the interpretation of the results. “Pleasantness” decisions of this sort have been used for over 30 years to probe “deep” or “semantic” knowledge [Warrington and Weiskrantz, 1968]. Each printed stimulus word was available for 3 sec followed by a 1 sec ISI, and each 10-word block lasted 40 sec. Subjects indicated their judgment of each word as pleasant or not by depressing one of two buttons (the “pleasant” button with the right hand or the “not pleasant” button with the left), and response and latency were recorded by the computer presenting the stimuli. Words were presented continuously, and blocks were presented in a fixed random order without a break between blocks of different categories. Subjects were

not informed that different categories of words were being administered. Each run included two blocks of each category of verb (four blocks of verbs in total). Each run also included six blocks of filler words (nouns), and three baseline blocks (including two blocks of pronounceable pseudoword stimuli and one block of pseudofont stimuli) interspersed among the blocks of verb stimuli. Three runs containing non-repeated stimuli were presented in total. Before each run, longitudinal magnetization was allowed to attain equilibrium while subjects were acclimated to the MRI environment during a 20 sec period of viewing the words "Get Ready" on the screen. Images corresponding to this period were discarded. Brief rest periods were included between runs.

Our stimulus presentation system (Epson 5000 LCD projector), compatible with high magnetic fields, back-projected the printed words onto a screen at the magnet bore. The subject viewed the screen through a system of mirrors. A portable computer (Macintosh 1400C) outside the magnet room used PsyScope presentation software [Cohen et al., 1993] to present stimuli and record response accuracy and latency. Subjects were familiarized with the task before entering the magnet bore, and the task was practiced by each subject.

Imaging data acquisition and statistical analysis

The experiment was carried out at 1.5 T on a GE Echosped scanner capable of ultrafast imaging. We used a standard clinical quadrature radiofrequency head coil. Firm foam padding was used to restrict head motion. Each imaging protocol began with a 10–15 min acquisition of 5 mm thick adjacent slices for determining regional anatomy, including sagittal localizer images (TR = 500 msec, TE = 10 msec, 192×256 matrix), T2-weighted axial images (FSE, TR = 2,000 msec, TE_{eff} = 85 msec), and T1-weighted axial images of slices used for fMRI anatomic localization (TR=600 msec, TE=14 msec, 192×256 matrix). Gradient echo echoplanar images were acquired for detection of alterations of blood oxygenation accompanying increased mental activity. All images were acquired with fat saturation, a rectangular FOV of 20×15 cm, flip angle of 90° , 5 mm slice thickness, an effective TE of 50 msec, and a 64×40 matrix, resulting in a voxel size of $3.75 \times 3.75 \times 5$ mm. The echoplanar acquisitions consisted of 18 contiguous slices in a transaxial plane covering most of the brain every 2 sec. A separate acquisition lasting 2 min was needed for phase maps to correct for distortion in echoplanar

images. Raw data were stored by the MRI computer on DAT tape and then processed off-line.

Initial data processing was carried out with Interactive Data Language (Research Systems) on a Sun (Santa Clara, CA) Ultra 60 workstation. Raw image data were reconstructed using a 2D FFT with a distortion correction to reduce artifact due to magnetic field inhomogeneities. Individual subject data were then prepared for pseudosubject analysis and analyzed statistically using statistical parametric mapping (SPM) developed by Wellcome Department of Cognitive Neurology [Frackowiak et al., 1997]. The SPM99 system, operating on a MatLab platform, combines raw difference images from individual subjects into a statistical t-map using the intersubject variance. Briefly, the images in each subject's time series were registered to the initial image in the series. The images were then aligned to a standard coordinate system [Talairach and Tournoux, 1988]. The data were spatially smoothed with a 12 mm Gaussian kernel to account for small variations in the location of activation across subjects, and temporal smoothing was conducted with a 2.8 sec kernel to account for small variations in the hemodynamic response function. The data were analyzed parametrically using *t*-test comparisons converted to z-scores for each compared voxel. We assessed activation associated with verbs compared to the baseline pseudoword-pseudofont stimuli because use of nouns as a baseline would be likely to reveal different patterns of activation depending on the specific features associated with the baseline words (we found little difference as a function of pseudoword or pseudofont baseline stimuli, and thus grouped these together as a single baseline). We also directly contrasted activation associated with the categories of verbs. We borrowed the statistical approach developed for so-called conjunction analysis to help assess differences between closely matched conditions [Price and Friston, 1997]. This analysis identifies the voxels that are significantly recruited in common across pairs of contrasts, in effect reducing the search space and optimizing the degrees of freedom for closely matched pairs of stimuli. For present purposes, we examined differences between verb subcategories in the context of a statistical "mask" defined by the "verb minus baseline" contrast.

RESULTS

Behavioral observations

Pleasantness judgments associated with each category of knowledge and latencies for making these

TABLE I. Mean ($\pm$ SD) pleasantness judgments and latencies for pleasantness judgments in motion and cognition verbs

Categories	Judgments ^a	Latencies
Motion	0.51 ($\pm$ 0.21)	1364 ($\pm$ 299)
Cognition	0.65 ($\pm$ 0.17)	1305 ($\pm$ 236)

^a Words were scored 1 if judged pleasant and 0 if judged not pleasant.

judgments are summarized in Table I. COGNITION verbs were judged to be more pleasant than MOTION verbs [$t(15)=3.87$; $P < 0.005$]. There were, however, no differences in the latency to respond during these pleasantness judgments [$t(15) = 1.50$; NS]. This suggests that a distinct pattern of neural recruitment for a category cannot be attributed to a difference in the relative effort involved in judging a category of verb knowledge.

Imaging observations

Table II provides the spatial coordinates of the peak anatomic recruitment within each significant cluster and summarizes the anatomic location of each significant cluster according to the normalized Talairach and Tournoux [1988] brain.

Figure 1 illustrates the contrast of all verbs minus the baseline of combined pseudowords and pseudofonts. Significant recruitment (at the $P < 0.001$ level, uncorrected) was seen in ventral occipital and temporal regions bilaterally (Brodmann area [BA] 17, 18, 19), with greater recruitment on the left than the right. Significant activation was also evident in left posterolateral temporal cortex (BA 22, 21, 37). Prefrontal cortex activation (BA 10, 9) was bilateral, more prominently on the left than the right, at the $P < 0.003$ level.

Panel A of Figure 2 illustrates the contrast of MOTION verbs minus COGNITION verbs. This comparison demonstrated recruitment centered in left ventral temporal-occipital cortex (BA 19). We also observed activation of bilateral prefrontal cortex (BA 10, 11) and caudate.

Panel B of Figure 2 illustrates the activation pattern associated with COGNITION verbs minus MOTION verbs. This contrast revealed significant recruitment of left posterolateral temporal cortex (BA 22, 21, 37).

DISCUSSION

We found that verbs recruit bilateral ventral temporal-occipital cortex, bilateral prefrontal cortex, and left posterolateral temporal cortex. This distribution of activation largely overlaps with the activation pattern for verbs described in previous studies [Perani et al., 1999; Martin et al., 1995; Warburton et al., 1996]. At first glance, inspection of the distinct activation patterns associated with each verb subcategory appears to be consistent with the “sensory-motor” account for the category-specific neural representation of verb knowledge: MOTION verbs were associated with left ventral temporal-occipital, bilateral prefrontal, and caudate recruitment. Closer inspection of our results, however, suggests that this interpretation is not so straightforward: COGNITION verbs with few sensory-motor features are associated with activation of left posterolateral temporal cortex, even though this region has been related to visual motion. We examine below the activation pattern associated with each subcategory of verb knowledge. By way of anticipation, we conclude that sources of knowledge beyond sensory-motor features are likely to contribute to the neural activation associated with some verb categories.

TABLE II. Locus and extent of peak activations in brain regions during pleasantness judgments of verbs

Contrast	Activation locus (BRODMANN area)	Co-ordinates			Z-value
		x	y	z	
All verbs minus baseline	Left posterolateral temporal (22, 21, 37)	-64	-48	12	3.63
	Bilateral prefrontal (10, 9)	-4	40	-12	2.72
	Bilateral ventral temporal-occipital (18, 19, 17)	0	-92	4	4.27
Motion verbs minus cognition verbs ^a	Left ventral temporal-occipital (19)	-8	-64	0	3.77
	Bilateral prefrontal (10, 11)	12	36	-12	3.15
	Bilateral caudate	16	16	20	3.46
Cognition verbs minus motion verbs ^a	Left posterolateral temporal (22, 21, 37)	-56	-68	8	3.06

^a These contrasts were performed borrowing the statistical procedure for a conjunction analysis, using [verbs minus baseline] as a statistical mask.

Figure 1.

Contrast of activation associated with all verb stimuli compared to a baseline including pronounceable pseudowords and pseudofonts.

MOTION verbs

Verbs of MOTION have relatively rich sensory-motor features. This appears to parallel the concrete nouns that are typically studied in neuroimaging assessments of category-specific lexical comprehension. Moreover, this raises the expectation that MOTION verbs are likely to have a pattern of activation similar to that associated with concrete nouns because both word subcategories denote observable objects/events. We found that MOTION verbs recruit ventral temporal-occipital cortex more in the left hemisphere than the right hemisphere, as well as bilateral prefrontal cortex and caudate. MOTION verbs have prominent

visual-perceptual features that may be responsible for recruitment of visual association cortex [Cappa et al., 1998; Chao et al., 1999; Damasio et al., 1996; Martin et al., 1996; Mummery et al., 1998; Perani et al., 1995], and are associated with features of action planning and execution that appear to recruit premotor and prefrontal cortices [Decety et al., 1994; Jeannerod et al., 1995; Rizzolatti et al., 1996a,b]. From the perspective of the “sensory-motor” hypothesis, the distribution of neural activation associated with MOTION verbs thus can be attributed to the same kind of sensory-motor features thought to contribute to the recruitment pattern seen for manufactured artifacts such as IMPLEMENTS.

Figure 2.

Contrasts of verb subcategories. **A:** MOTION verbs – COGNITION verbs. **B:** COGNITION verbs – MOTION verbs. The locus and distribution of peak activation for each recruited region are summarized in Table II. The contrasts of the two verb subcategories were derived by borrowing the statistical procedure for conjunction analysis, with (verbs – baseline) as the conjoined contrast acting as a statistical “mask”.

Many functional neuroimaging studies of manufactured artifacts in fact demonstrate recruitment of premotor/prefrontal and posterolateral temporal cortices [Cappa et al., 1998; Chao et al., 1999; Damasio et al., 1996; Martin et al., 1996; Mummery et al., 1998; Perani et al., 1995]. Our findings are consistent with studies reported by Chao et al. [1999] and Martin et al. [1996] that emphasize the role of ventral temporal-occipital activation in supporting visual-perceptual features. We did not, however, observe activation for MOTION verbs in a posterolateral temporal-occipital distribution that has been associated with the perception of visual motion [Bonda et al., 1996; de Jong et al., 1994; Kourtzi and Kanwisher, 2000; Patzwahl et al., 1996; Puce et al., 1998]. There is reason to believe that activation for MOTION verbs may not replicate activation associated with manufactured artifacts such as IMPLEMENTS. For example, direct comparisons of behavioral judgments of MOTION verbs, manufactured artifacts and natural kinds were assessed in three patients with relative sparing of action verb naming and three patients with relatively impaired action verb naming [Bird et al., 2000]. These investigators reported that the “verb-spared” patients had more difficulty naming natural kinds than manufactured artifacts, and that their definitions of objects include fewer sensory-motor features. The naming deficit in the “verb-impaired” patients, however, was not associated with difficulty naming manufactured artifacts like IMPLEMENTS. According to Bird et al. [2000], verb difficulties are related in part to the reduced imageability of these verbs compared to manufactured artifacts, and thus may explain in part the absence of left posterolateral temporal recruitment during MOTION verb judgments in the present experiment. Regardless of the specific basis for these noun-verb differences, direct contrast of MOTION verbs and IMPLEMENT nouns shows distinct activation patterns as well [Koenig et al., 2001]. Additional work is needed to establish the precise nature of the sensory-motor features that contribute to concrete nouns such as IMPLEMENTS and related action verbs such as verbs of MOTION.

We also observed prefrontal and caudate recruitment in association with MOTION verbs. These brain structures are part of a frontal-striatal-thalamic loop that has been implicated in motor functions [Alexander et al., 1990]. One possible explanation for frontal-caudate recruitment is associated with the “sensory-motor” hypothesis. Specifically, prefrontal recruitment may be related to the knowledge of action features associated with both MOTION verbs and manufactured artifacts such as IMPLEMENTS. The activation may be relatively more anterior than that

typically associated with manufactured artifacts such as IMPLEMENTS because of the relatively more complex nature of lexical knowledge associated with verbs compared to nouns [Koechlin et al., 1999, 2000]. Caudate recruitment appears to be associated only with MOTION verbs but not manufactured artifacts, and caudate activation may support the actual motor features that are associated only with MOTION verbs but not with IMPLEMENTS. The right-lateralized predominance of caudate recruitment may reflect in part the spatial properties of MOTION verbs [Jackendoff, 1983]. The right hemispheric involvement is consistent with a report of two patients with right frontal disease who show deficits for ACTION verbs compared to concrete nouns [Neininger and Pulvermuller, 2001].

The frontal-striatal loop is also implicated more directly in cognitive processes such as the executive resources that contribute to working memory [Braver et al., 2001; Cohen et al., 1994; Dagher et al., 1999; Grafman et al., 1990; Owen et al., 1998; Smith and Jonides, 1999], and another account relates frontal-caudate activation to the complex nature of thematic roles that are associated with verbs of MOTION. MOTION verbs are typically related to a variety of direct or indirect objects, corresponding to the potentially large array of thematic roles with which a verb can be linked. Some evidence to support this claim comes from the observation that verbs with larger numbers of optional thematic roles are more difficult to understand than verbs with fewer optional thematic roles [Shapiro et al., 1987, 1993]. Consistent with this potential need to manage a complex network of optional thematic roles, several functional neuroimaging studies demonstrate recruitment in a frontal-caudate distribution during resource-demanding verbal measures [Cooke et al., 2000; Poldrack et al., 1999; Rypma et al., 1999]. This is less likely to account for frontal-caudate recruitment only during presentation of MOTION verbs, however, given the apparently equal levels of difficulty for MOTION verbs and COGNITION verbs suggested by the equivalent latency measures.

Another less likely possibility is that medial prefrontal recruitment is related to the nature of the probe we used to investigate verb meaning. "Pleasantness" was used recently to probe self-referential mental activity during judgments of pleasant and unpleasant pictures [Gusnard et al., 2001]. Medial prefrontal activity was associated with "pleasantness" ratings. There are several reasons to doubt this account. For one, direct contrast of MOTION verbs and COGNITION verbs should minimize this component of our task because "pleasantness" is probed for both categories of verbs. Even if "pleasantness" is associated

unequally with these two verb categories, Gusnard et al. [2001] would predict medial prefrontal activation for the more affectively charged COGNITION verbs (i.e., "pleasantness" judgments that deviate more from 0.5), when in fact we find prefrontal activity associated with MOTION verbs rather than COGNITION verbs. Finally, we do not see prefrontal activation for all categories of nouns we probed with the "pleasantness" task [Grossman et al., in press]. In like manner, the association of prefrontal activation with novel, attention-demanding tasks and materials that require the integration of cognitive and emotional attributes [Drevets and Raichle, 1998; Shulman et al., 1997; Simpson et al., 2001] is unlikely to explain the preferential association of this region with only one verb category. Additional work is needed to determine the precise basis for frontal-caudate recruitment during lexical processing.

COGNITION verbs

Although some evidence consistent with the "sensory-motor" hypothesis may be derived from the pattern of neural activation associated with MOTION verbs, inspection of brain activation during presentation of COGNITION verbs is less supportive of a strong version of the "sensory-motor" hypothesis that attempts to account for the meaning of all verbs. Verbs of COGNITION are associated with recruitment of left posterolateral temporal cortex. Other studies investigating the neural basis for word comprehension that use MOTION verbs as stimuli also recruit this posterolateral temporal region [Fiez et al., 1996; Martin et al., 1995; Perani et al., 1999; Warburton et al., 1996]. This is attributed to visual-perceptual features such as motion that are a property of the stimulus word and that recruit visual association cortex in a posterolateral temporal-occipital distribution [Bonda et al., 1996; de Jong et al., 1994; Kourtzi et al., 2000; Patzwahl et al., 1996; Puce et al., 1998]. The pattern of activation associated with these findings is interpreted to support the "sensory-motor" approach to the neural representation of verb meaning. One problem with this line of reasoning is that these observations are based primarily on verbs associated with observable events, whereas verbs of COGNITION such as "think" and "speculate" are quite impoverished in their visual-perceptual and motor-action features.

It is possible to couch differences in the distribution of neural recruitment for MOTION verbs and COGNITION verbs in the context of the "dual coding" hypothesis [Kounios and Holcomb, 2000; Paivio, 1971, 1978, 1991]. According to this approach, concrete words can be

encoded in a visual, image-based manner and as verbal-propositional knowledge, whereas abstract words can be encoded only in a verbal-propositional manner. Analogously, the sensory-motor features of MOTION verbs may allow these words to be encoded by the visual, image-based system in visual association cortex and as verbal-propositional knowledge represented in peri-Sylvian regions of the left hemisphere, whereas encoding of COGNITION verbs may be largely restricted to verbal-propositional knowledge. One problem with this proposal is that there is no brain area encoding verbal-propositional knowledge that is recruited for both categories of verbs. Moreover, this kind of approach would have difficulty explaining "reversal of the concreteness effect" seen in some patients [Breedin et al., 1995; Sirigu et al., 1991; Warrington, 1975, 1984]. Based on observations such as these, COGNITION verbs appear to possess features that are relatively unique to abstract words and that are not explained by the general degradation of sensory-motor feature knowledge. The feature distinct to abstract words such as COGNITION verbs may be the elaborated set of semantic relations characteristic of the concepts underlying abstract words [Gentner, 1981; Jackendoff, 1990; Pinker, 1989], and it is the processing of the complex interaction of propositional features that may be responsible for left posterolateral temporal activation. This would be consistent with the neuroanatomic connectivity pattern of posterolateral temporal cortex, a supramodal region that has reciprocal connections with multiple association cortices [Mesulam, 1985]. ABSTRACT nouns recruit left posterolateral temporal cortex and prefrontal cortex compared to pronounceable pseudowords and compared to concrete nouns such as ANIMALS [Beauregard et al., 1997; Grossman et al., in press; Perani et al., 1999]. We speculated that the anatomic connectivity pattern of this posterior supramodal association region is ideally suited to the collection and organization of the propositional knowledge associated with abstract word meaning that is widely distributed throughout association cortices [Grossman et al., in press]. This account may help explain left posterolateral temporal recruitment for COGNITION verbs as well.

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