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HOW NECESSARY ARE THE STRIPES OF A TIGER? DIAGNOSTIC AND CHARACTERISTIC FEATURES IN AN fMRI STUDY OF WORD MEANING

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Abstract

This study contrasted two approaches to word meaning: The statistically-determined role of high-contribution features like *striped* in the meaning of complex nouns like “tiger” typically used in studies of semantic memory, and the contribution of diagnostic features like *parent’s brother* that play a critical role in the meaning of nominal kinds like “uncle.” fMRI monitored regional brain activity while participants read complex noun descriptions consisting of statistically high-contribution and low-contribution features; and nominal kind descriptions consisting of diagnostic and characteristic features. We found different patterns of activation depending on the type of noun and the type of feature contributing to the noun. Complex nouns recruited significantly greater bilateral superior temporal and left prefrontal activation compared to nominal kind nouns, while nominal kind nouns activated bilateral medial parietal and right inferior parietal regions more than complex nouns. Moreover, features making a statistically high contribution to complex noun meaning activated right inferior frontal cortex relative to low-contribution features, while diagnostic features of nominal kinds activated left dorsolateral prefrontal and right parietal regions more than characteristic features. These findings are consistent with the hypothesis that at least two different neural mechanisms appear to support word meaning: One driven by a statistically-determined approach to feature knowledge, and the other sensitive to the qualitatively critical role that a specific diagnostic feature plays in word meaning.

Keywords

semantic memory; fMRI

INTRODUCTION

Recent studies of semantic memory have focused on the relatively distinct anatomic distributions of different categories of knowledge (Martin, Ungerleider, & Haxby, 2000). However, this approach does not appear to explain fully the neural basis for word meaning (Farah & Aguirre, 1999; Grossman & Koenig, 2001; Joseph, 2001; Thompson-Schill, 2003), prompting alternate approaches to the study of semantic memory. In the work presented below, we examined the hypothesis that there are at least two approaches to word meaning. We

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investigated the statistically-determined role of high-contribution features and low-contribution features in the meaning of complex nouns typically used in studies of semantic memory. We contrasted these complex nouns with nominal kinds, a class of nouns where a specific diagnostic feature appears to play a relatively critical role as an attribute of the word's meaning, and characteristic features embellish but do not determine word meaning.

There is a long history emphasizing the role of feature knowledge in word meaning (Fodor, 1977; Katz & Fodor, 1963; Katz, 1966). Recently, functional neuroimaging studies have focused on modality-specific models concerned with the hemispheric representation of visual and verbal knowledge (Binder, Westbury, McKiernan, Possing, & Medler, 2005; Noppeney & Price, 2003; Perani et al., 1999; Vandenberghe, Price, Wise, Josephs, & Frackowiak, 1996), and the representation of knowledge based on semantic category taxonomy (Grossman et al., 2002a; Mummery, Patterson, Hodges, & Wise, 1996; Perani et al., 1995). Perhaps the most frequently cited account theorizes that activations for semantic features of concepts are stored in brain areas adjacent to regions that are important for perceiving the same properties (Cappa, Perani, Schnur, Tettamanti, & Fazio, 1998; Chao, Haxby, & Martin, 1999; Grabowski, Damasio, & Damasio, 1998; Kellenbach, Brett, & Patterson, 2001; Martin, Wiggs, Ungerleider, & Haxby, 1996; Moore & Price, 1999; Perani et al., 1995; Smith et al., 2001; Thompson-Schill, Aguirre, D'Esposito, & Farah, 1999). Color and form features for ANIMALS (we use capitals to indicate a category of knowledge) are thought to activate ventral temporal-occipital cortex because these areas are important for perceiving these visual properties, for example, while visual motion and action features associated with TOOLS activate lateral temporal-parietal-occipital cortex and motor association cortex because of the role of these brain areas in perceiving these visual-motor properties (Chao et al., 1999; Martin et al., 2000). However, the anatomic correspondence between activation for perceptual features purportedly important for a semantic category and the corresponding sensory-motor regions is only partial (Kellenbach et al., 2001; Noppeney & Price, 2002), and overlap may be seen between concepts as distinct as ANIMAL and ABSTRACT nouns (Beauregard et al., 1997; Binder et al., 2005; Grossman et al., 2002a; Kiehl et al., 1999; Noppeney et al., 2002).

While the sensory-motor features associated with a concrete noun undoubtedly contribute to word meaning, the present study examines the possibility that different kinds of features contribute to the meaning of qualitatively distinct classes of words. From this perspective, one kind of features appears to make a statistically-determined contribution to semantic memory. Some of these features are thought to play a "high-contribution" role in the meaning of a word since many people associate this kind of feature with its meaning. Other features play a "low-contribution" role since fewer people associate this kind of feature with word meaning. Consider "tiger." Many associate "tiger" with *stripes* (we use italics to indicate a feature), suggesting that this may be a high-contribution feature for the meaning of "tiger." However, there is nothing necessary about the *stripes* of "tiger." Likewise, the distinction between a complex noun's high-contribution features and low-contribution features is one of degree. The *stripes* of a "tiger" may be held by many to make an important contribution to the meaning of "tiger" compared to its *orange color*, *Asian habitat*, or *sharp teeth*, but others may consider its *orange color* to be relatively more important. While many features may be associated with the meaning of a word, it is difficult to assert that any one feature of a complex noun like "tiger" contributes necessarily to its meaning with anything more than a statistical level of probability.

Contrast complex nouns such as this with the class of nouns that are identified by the presence of a diagnostic feature that plays a disproportionately important role in determining its meaning. These nouns are known as "nominal kinds." An example of a nominal kind is a kinship term like "uncle." The diagnostic feature of "uncle" is a *parent's brother*. A *parent's sister* or a *brother's son* is not an uncle. *Friendliness, joining the family for holiday gatherings*, and

bringing presents on birthdays may be characteristic features of “uncle,” but none of these features would be considered potentially diagnostic of “uncle.” A *mean, stingy hermit* would be no less of an “uncle,” as long as he is a *parent's brother*. The wide use of kinship terms in many human societies emphasizes that this class of nouns is not unique to western cultures. While nominal kinds often tend to be abstract, other nominal kinds may be less so (e.g. “island” is a body of land totally surrounded by water). There are specific circumstances where the traditional meaning of a nominal kind like “uncle” may be stretched, such as following a divorce or when denoting a metaphoric relationship with an esteemed individual who is “like an uncle to me.” While observations such as these underline that there is no absolute distinction between nominal kinds and complex nouns, even the special conditions that blunt the status of a diagnostic feature of a nominal kind derive their power from the traditional sense in which an “uncle” has a particular meaning based on the relatively diagnostic value of its critical feature. In general, there are no such diagnostic features associated with complex nouns such as “tiger” or “hammer” that are used in most semantic memory research.

In this study, we examined whether there are two approaches to word meaning. We monitored regional brain activity while subjects read descriptions of complex nouns or nominal kind nouns, and then decided whether the description accurately portrayed a target noun. Each description consisted of a diagnostic or high-contribution feature and several characteristic or low-contribution features. We expected different activation patterns for nominal kinds compared to complex nouns, and for each type of feature contributing to these noun categories. Specifically, subjects may recall previously encountered exemplars of a nominal kind because a diagnostic feature is a reliable attribute of the word's exemplars. Independent of any sensory-motor property, successful recall appears to depend in part on medial parietal cortex (Buckner, Koutsaal, Schacter, Wagner, & Rosen, 1998b; Buckner & Koutsaal, 1998a; Kapur, Craik, Jones, & Brown, 1995; Lepage, Ghaffar, Nyberg, & Tulving, 2002; Nestor, Fryer, & Hodges, 2006; Rugg et al., 1998). Moreover, since this diagnostic feature is present so reliably in a noun's exemplars, we reasoned that decisions about word meaning would be reliably biased by such a diagnostic feature. The implementation of this bias is likely to depend on decision-making that is supported in part by dorsolateral prefrontal cortex (Badre & Wagner, 2004; Botvinick, Braver, Barch, Carter, & Cohen, 2001; Carter et al., 2000; MacDonald, Cohen, Stenger, & Carter, 2000). The similarity-based categorization process involved in comparing the description to the mental representation of the target exemplars is likely to be mediated in part by inferior parietal cortex (Grossman et al., 2002b; Koenig et al., 2005). By comparison, a feature is associated with the meaning of a complex noun only in a statistical sense, so a broad array of feature knowledge is likely to be activated, such as may be represented in temporal cortex (Cappa et al., 1998; Chao et al., 1999; Grabowski et al., 1998; Kellenbach et al., 2001; Martin et al., 1996; Moore et al., 1999; Perani et al., 1995; Smith et al., 2001; Thompson-Schill et al., 1999).

METHODS

Subjects

We assessed 25 young healthy adult participants [mean ($\pm$ S.D.) age = 24.13 ($\pm$ 3.4) years; mean ($\pm$ S.D.) education = 16.94 ($\pm$ 2.1) years], including 11 males and 14 females. All were right-handed native English-speakers. Informed consent was obtained from all individuals according to a protocol approved by the Institutional Review Board at the University of Pennsylvania.

Materials

We identified 16 concepts taken from complex noun categories that are typically used in studies of semantic memory, including ANIMALS and TOOLS. Based on developmental work (Keil,

1989), we also identified 12 concepts taken from categories that are good examples of nominal kinds: KINSHIP terms and MORAL terms. Four additional nominal kind stimuli (i.e. MEALS) had been eliminated from analyses since behavioral assessments showed that they were not treated reliably as nominal kinds.

The target nominal kinds and complex nouns were matched in their frequency of occurrence [$F(3,12)=1.64$; ns] and familiarity [$F(3,12)=0.93$; ns], although there was a marginal difference in imageability [$F(3,12)=3.59$; $p<0.05$] that was due to the reduced imageability of MORAL relative to ANIMAL [$t(6)=2.58$; $p<0.05$] and TOOL [$t(6)=2.57$; $p<0.05$] terms. A diagnostic feature was identified for each nominal kind, and a high-contribution feature was identified for each complex noun. These features were taken from Keil (1989) or were developed from extensive pilot testing, where 15 young adults were asked to provide the single most “defining” feature of each target noun. Additional diagnostic and high-contribution features, or other target nouns, were identified until a reliable set of these noun-feature pairs was created. We identified five characteristic or low-contribution features associated with each nominal kind and each complex noun in a similar manner. These features, although associated with the target noun, were not thought to be diagnostic or high-contribution features of the noun in the sense that their absence would not exclude an exemplar from being a member of the associated category (e.g. *friendly* uncle; *sweet* apple). Following Keil (1989), an example of a nominal kind moral stimulus is: STEAL? Don is mean. He wears old dark clothes. Liz has a new TV. Don takes her TV without asking. Don is evil. He carries a gun. Did Don STEAL? An example of a complex noun tool stimulus is: SCISSORS? This tool is sharp. Sue holds it in one hand. It’s used to cut paper. It’s used in schools. It has two blades. The blades are metal. Is this tool SCISSORS? These feature descriptions were matched in their frequency [$F(3,12)=2.83$; ns] and familiarity [$F(3,12)=0.39$; ns] across categories, while imageability differed across categories [$F(3,12)=10.13$; $p<0.01$] due to the reduced imageability of nominal kinds. Diagnostic/high-contribution features matched characteristic/low-contribution features for frequency [$F(1,94)=1.25$; ns], and diagnostic and high-contribution features were matched for word length [$F(3,12)=1.76$; ns] and syllable length [$F(3,12)=0.65$; ns]. Eleven young control subjects, given all of the features associated with the description of a target word, reliably identified the diagnostic feature (96.6% accurate) and the high-contribution feature (92.1% accurate) as playing the most important role in determining the meaning of its target noun, and this was equally reliable for nominal kinds and complex nouns [$t(10)=1.39$; ns]. Finally, we identified a feature for each noun thought to exclude the description as an exemplar since it could not be a property of that noun (e.g. an “uncle” could not be a *female*, a “tiger” could not have a *trunk*) and a set of five features thought to be uncharacteristic or atypical of each target noun. Pilot testing in 15 young subjects indicated that descriptions where the features are inconsistent with the target noun are statistically more likely to be rejected. From these features, four types of descriptions were created for each target noun: For nominal kinds, these included one diagnostic feature paired with five characteristic features, one diagnostic feature paired with five uncharacteristic features, one exclusionary diagnostic feature paired with five characteristic features, and one exclusionary diagnostic feature paired with five uncharacteristic features; for complex nouns, these included one high-contribution feature paired with five low-contribution features, one exclusionary feature paired with five low-contribution features, one high-contribution feature paired with five atypical features, and one exclusionary feature paired with five atypical features. The image analyses in this study focused exclusively on the activation occurring during the presentation of the diagnostic/high-contribution features and the characteristic/low-contribution features positively associated with the target noun, while stimuli with exclusionary and uncharacteristic/atypical features were omitted from further analysis. The true descriptions of the target complex nouns [mean ($\pm$ S.D.)=85.2% ($\pm$ 7.5) correct; mean events/subject=82.56] and the target nominal kind nouns [mean ($\pm$ S.D.)=86.6% ($\pm$ 7.4) correct; mean events/subject=78.80] were identified with equal

levels of accuracy by the subjects [$F(1,24)=.71$; ns]. During the imaging analyses, we excluded from consideration the stimuli that were judged incorrectly.

Procedure

On each trial, subjects first saw the printed target word for 3 sec at the top of the screen, presented by projector (Epson 8100 LCD) to a subject in the magnet bore through a series of mirrors. Then the six brief, written, feature descriptions were presented one at a time. The features accumulated beneath the target noun, with a 3 sec stimulus onset asynchrony. The order of presentation of the diagnostic/high-characteristic feature was pseudorandom such that this feature occupied each ordinal position of a description an equal number of times, and these items were randomly distributed among the other stimulus items throughout the study. Subjects were not told how many features may not be consistent with the target noun in any untrue noun description. After presentation of the features, subjects saw a written probe (the target noun with a question mark), and subjects were instructed to decide whether the presented features accurately described the target noun. Twelve seconds after the second presentation of the target noun, the next trial began. One half of the subjects were randomly designated to see these stimuli under rule-based categorization instructions, and one half under similarity-based instructions. For the rule-based condition, subjects were instructed that roughly half of the descriptions accurately described the target noun. They were told to consider the descriptions carefully, and were asked to identify the accurate descriptions of the target noun. For the similarity-based condition, subjects were told that the descriptions overall described the target noun, and were asked to decide whether a description reasonably described the target noun. Analyses of the activation differences between rule-based and similarity-based conditions for diagnostic features compared to characteristic features of nominal kinds or complex categories did not reveal statistically significant effects. The activations associated with rule-based and similarity-based judgments of the complex and nominal noun descriptions with exclusionary features are presented elsewhere. Subjects were given several practice trials prior to performing the task in the magnet.

Imaging procedure and analysis

The experiment was carried out at 3T on a Siemens Trio scanner capable of ultrafast imaging. Firm foam padding was used to restrict head motion. Each imaging study began with a 10–15 min 3D MPRAGE protocol (TR=1620 msec, TE=3 msec, flip angle=15 degrees, 1 mm slice thickness, 192 x 256 matrix) with a rectangular field of view giving an in-plane resolution of 1 mm isotropic voxels for determining regional anatomy, including sagittal localizer images and axial images. BOLD fMRI images were then acquired to detect alterations in blood oxygenation accompanying increased mental activity. All images were acquired with fat saturation, 3 mm isotropic voxels, flip angle of 15°, TR=3000, TE_{eff}= 30 msec, and a 64 x 64 matrix, with prospective motion correction, acquiring 45 axial slices 3 mm in thickness through the entire brain every 3 sec. Raw data were transferred from the MRI computer to CD and 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 procedure that minimized artifact due to magnetic field inhomogeneities. Individual subject data were then prepared for statistical parametric mapping (SPM 99) developed by the Wellcome Department of Cognitive Neurology (Frackowiak, Friston, Frith, Dolan, & Mazziotta, 1997). This system, operating on a MatLab platform, combines raw images from subjects into a statistical t map. 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 & Tournoux, 1988). The data were spatially smoothed with an 8 mm Gaussian kernel

to account for small variations in the location of activation and sulcal anatomy across subjects. Low-pass temporal filtering was implemented by controlling auto-correlation with a first-order auto-regressive method.

We used an event-related approach to data acquisition. The random order of target noun presentation, and the randomization of feature order within each target noun description, allowed us to group and compare images corresponding to specific classes of nouns and features so that we could obtain an estimate of the independent contribution of each variable of interest in this study. After eliminating the descriptions where subjects did not correctly judge the truth of the description for the target noun, we identified all of the remaining diagnostic/high-contribution features and characteristic/low-contribution features of complex nouns and nominal kinds positively associated with the target word. A random-effects analysis was used. To isolate the BOLD signal for each condition of interest, we convolved the signal with a standardized hemodynamic response function (HRF) and the time derivative for each onset in SPM99. Each contrast of interest was performed in each individual subject, and these contrasts were then fed into a second-level analysis to examine group-wide differences. Statistical contrasts first evaluated the diagnostic/high-contribution features and characteristic/low-contribution features grouped across complex nouns and nominal kind nouns, and the complex nouns and nominal kind nouns grouped across the diagnostic/high-contribution features and characteristic/low-contribution features. Next, we compared the diagnostic/high-contribution features and the characteristic/low-contribution features for the complex nouns and for the nominal kind nouns. The statistical contrasts were converted to z-scores for each compared voxel, and the corresponding T-scores are reported. Peak voxels reported below were converted from MNI coordinates to Talairach coordinates. Voxel-level analyses used a statistical threshold of $p < 0.05$ corrected for multiple comparisons, and all reported peak voxels were from clusters significant in a cluster-level analysis at the $p < 0.05$ level corrected for multiple comparisons.

RESULTS

Activations associated with descriptions of complex nouns differ from activations for nominal kind nouns. Table 1 summarizes the activations associated with complex nouns and nominal kind nouns across diagnostic/high-contribution features and characteristic/low-contribution features. Contrasts of these activations are illustrated in Figure 1. Figure 1 Panel A shows greater activation for complex noun descriptions than nominal kind descriptions in left dorsolateral prefrontal cortex and bilateral superior temporal regions. Nominal kind descriptions show bilateral medial parietal and right inferior parietal-posterolateral temporal activation relative to complex nouns, as illustrated in Figure 1 Panel B.

Diagnostic/high-contribution features evoked much more activation than characteristic/low-contribution features, as summarized in Table 1. The direct contrast of diagnostic/high-contribution features relative to characteristic/low-contribution features, across complex nouns and nominal kinds, reveals significant recruitment in dorsal anterior cingulate cortex and thalamus bilaterally (Figure 1 Panel C). There were no areas of statistically greater activation associated with characteristic/low-contribution features compared to diagnostic/high-contribution features.

Diagnostic features of nominal kind nouns and high-contribution features of complex nouns appear to have different recruitment patterns. These activations are summarized in Table 2. Figure 2 Panel A shows a direct contrast of diagnostic features compared to characteristic features for nominal kind nouns. We found significantly greater recruitment for diagnostic features in left dorsolateral prefrontal and right parietal regions. For characteristic features

minus diagnostic features of nominal kinds, we found greater activation in right ventral temporal cortex (not illustrated). By comparison, Figure 2 Panel B illustrates the direct contrast of high-contribution features and low-contribution features in descriptions of complex nouns. We found significant activation of right inferior frontal cortex for high-contribution features. The contrast of low-contribution minus high-contribution features did not reveal significant differences.

DISCUSSION

Our observations are consistent with the hypothesis that there are at least two routes to word meaning. One approach appears to be statistically-determined. This has been used to advantage in computationally-based, distributed models of semantic memory (McClelland & Rogers, 2003). From this perspective, complex nouns are sensitive to the graded probability that a feature contributes to word meaning since certain features appear carry relatively greater weight than others in determining the meaning of such a word. Yet there is considerable variability in the relative importance and reliable presence of any one of these features in an exemplar of the word. A second mechanism, more closely related to structuralist accounts (Fodor, 1977; Katz et al., 1963; Katz, 1966), emphasizes the specific content of some features since they play a qualitatively distinct role in semantic memory. This can be seen in the class of nouns known as nominal kinds. Unlike the statistical relationship of a feature with a complex noun, a diagnostic feature appears to make a qualitatively distinct contribution to the meaning of a nominal kind. Our findings show that complex and nominal kind nouns are associated with distinct patterns of brain activity, consistent with the hypothesis that there are two routes to word meaning. We also find that diagnostic/high-contribution features show greater activation than characteristic/low-contribution features, consistent with the prominent role that the former class of features plays in word meaning. Finally, even though diagnostic features and high-contribution features play an important role in word meaning, the pattern of activation associated with these features varies depending on the specific nature of the noun to which these features contribute. This is consistent with the qualitatively distinct role that these features play relative to their nouns. We discuss below the nature of the activations associated with complex nouns compared to nominal kinds, and the distinct role that diagnostic features appear to play in word meaning relative to the statistically-determined role of high-contribution features.

Complex nouns and nominal kind nouns have distinct activation patterns. Complex nouns such as ANIMALS and TOOLS activate left frontal and bilateral temporal regions relative to nominal kinds. Although several surveys describe poor consistency in the distribution of activation associated with a specific semantic category across neuroimaging studies of semantic memory (Farah et al., 1999; Grossman et al., 2001; Joseph, 2001; Thompson-Schill, 2003), many imaging studies of semantic memory show dorsolateral prefrontal and lateral temporal activation. Anatomic studies indicate that these are multimodal association cortical regions (Mesulam, 2000; Mesulam, van Hoesen, Pandya, & Geschwind, 1977; Pandya & Kuypers, 1969; Pandya & Yeterian, 1996), so we doubt that these activations depend exclusively on the specific sensory-motor content of a semantic category since they do not have the same connectivity patterns or cytoarchitectonic properties as the sensory-motor association areas implicated in the storage of sensory-motor semantic features. Likewise, dorsolateral prefrontal and lateral temporal activation is also seen for ABSTRACT nouns (Beauregard et al., 1997; Binder et al., 2005; Grossman et al., 2002a; Kiehl et al., 1999; Noppeney et al., 2002). It is also unlikely that temporal activation is due to some property of the words used in this study since both these and nominal kind stimuli used similar lexical information, and descriptions were matched for word length and syllable length. Given the relatively anterior distribution of activation in the temporal lobe, one possibility is that these activations reflect

modality-neutral representations of concepts, such as may be compromised in patients with semantic dementia (Lambon Ralph, McClelland, Patterson, Galton, & Hodges, 2001; Rogers et al., 2004; Tyler et al., 2003; Williams, Nestor, & Hodges, 2005). Alternately, studies examining categorization of familiar objects and newly-acquired concepts in healthy adults and patients with neurodegenerative diseases suggest that these multimodal brain regions synthesize distributed feature knowledge into a coherent concept through categorization processes in semantic memory (Grossman et al., 2002b; Grossman et al., 2003; Koenig et al., 2005; Koenig, Smith, & Grossman, 2006). We attempted to examine this factor experimentally by administering these object descriptions under rule-based or similarity-based instructions, but we did not find a statistically significant effect. We suspect that this is due in part to the likelihood that nominal kinds are in some sense inherently rule-based, thereby obscuring the effect of instruction. Analyses of partial foils, pitting selective violations of diagnostic feature and characteristic feature accuracy against each other, will be useful for studying categorization processes but are beyond the scope of the present report.

Regardless of the basis for these frontal and temporal activations, this recruitment pattern for complex nouns differs from the significant medial parietal and lateral temporal-parietal activation associated with nominal kinds. We believe that medial parietal activation reflects the distinct nature of the features contributing to the meaning of a nominal kind compared to a complex noun. From this perspective, a diagnostic feature is a relatively reliable and consistent property of a nominal kind, and recall of such a feature from previous experience would be a useful guide to word meaning. By comparison, a high-contribution feature is less reliably present in any given exemplar of a complex noun. This medial parietal region has been associated with successful recall of previously experienced material (Buckner et al., 1998a; Buckner et al., 1998b; Kapur et al., 1995; Lepage et al., 2002; Rugg et al., 1998), including recall of remotely acquired material (Gilboa, Winocur, Grady, Hevenor, & Moscovitch, 2004), and independent of imagery (Krause et al., 1999; Schmidt, 2002). Medial parietal activation thus may support recall of previously encountered exemplars of a nominal kind.

Right inferior parietal activation also may be related to the distinct nature of the features contributing to nominal kinds. One possibility is that coarse coding may be needed to support critical semantic feature knowledge that is only present in nominal kinds, and coarse coding appears to depend on right hemisphere activation (Beeman et al., 1994; Grossman et al., 2002a). Right hemisphere activation is reported in many studies of semantic memory, perhaps reflecting the concrete nature of these stimuli from a dual coding perspective (Binder et al., 2005; Noppeney et al., 2003; Perani et al., 1999; Vandenberghe et al., 1996), although this would not explain why this activation was seen for nominal kinds relative to complex nouns. We doubt that parietal activation is supporting working memory to maintain features in an active state during the presentation of the description (Smith, Jonides, Marshuetz, & Koeppe, 1998; Smith, Marshuetz, & Geva, 2002) since this would not explain why activation during these verbal descriptions is seen in the right hemisphere that is usually recruited for visual-spatial working memory (Courtney, Ungerleider, Keil, & Haxby, 1996; Grady et al., 1998; Jonides et al., 1993; Smith, Jonides, & Koeppe, 1996). We also doubt that this is related to the reduced imageability of the nominal kinds relative to the complex nouns since other work describes significantly greater parietal activation for concrete nouns relative to abstract nouns (Binder et al., 2005), and several reports of fMRI studies describe parietal activation during visuospatial imagery tasks (Knauff, Fangmeier, Ruff, & Johnson-Laird, 2003).

A direct comparison of diagnostic/high-contribution features and characteristic/low-contribution features is consistent with the claim that all features are not necessarily equivalent, and that some features play a much more prominent role in word meaning than others. Diagnostic/high-contribution features activate bilateral dorsal anterior cingulate cortex and

thalamus. These areas are both associated with selective attention (Frith & Friston, 1996; Goldman-Rakic, 1995; LaBerge, 1995; Shulman et al., 1997). Thalamic activation may be due in part to the regulation of attention to a particular sensory-motor processing stream (Frith et al., 1996; Goldman-Rakic, 1995; LaBerge, 1995; Shulman et al., 1997). Lesion studies (Nadeau & Crosson, 1997; Raymer, Moberg, Crosson, Nadeau, & Gonzalez-Rothi, 1997) and fMRI work (Kraut et al., 2002) implicate the thalamus in semantic memory. Dorsal anterior cingulate cortex may make a higher-level contribution to selective attention by detecting a conflict between competing choices (Benedict et al., 1998; Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999; Botvinick, Cohen, & Carter, 2004; Carter et al., 2000; Corbetta, Miezin, Shulman, & Petersen, 1993; MacDonald et al., 2000; Pardo, Pardo, Janer, & Raichle, 1990). Dorsal anterior cingulate cortex thus may support detecting the presence of the diagnostic/high-contribution features in the presented descriptions. It is difficult to attribute greater activation for diagnostic/high-contribution features to their sensory-motor content since the characteristic/low-contribution features are taken from descriptions of the same target nouns. Pilot data indicated that subjects easily distinguish between diagnostic/high-contribution features and characteristic/low-contribution features, and these classes of features also are matched for frequency and familiarity. We limit our analysis to activation associated with features correctly associated with the target concept, and analyze only the stimuli that had been judged correctly, so it is unlikely that differential knowledge of these features can explain greater activation for diagnostic/high-contribution features than characteristic/low-contribution features.

We do not observe significantly greater activation for characteristic/low-contribution features than diagnostic/high-contribution features. This is not to say that characteristic/low-contribution features are not associated with cortical activation, since Table 1 shows that this class of semantic features does demonstrate occipital recruitment relative to a weak baseline, possibly related to mental imagery. We cannot rule out that there is insufficient power to detect the activations associated with a characteristic/low-contribution feature, although we studied a large number of subjects. It is also possible that a particular quality of characteristic/low-contribution features – such as the lower semantic association of these features with the target noun relative to the higher association of diagnostic and high-contribution features – plays a role in their relatively limited activation. A negative finding such as this must be interpreted cautiously, but the observation of modest activation for characteristic/low-contribution features seems to emphasize the relatively important role that a diagnostic/high-contribution feature plays in the interpretation of a word's meaning.

While both diagnostic and high-contribution features play a disproportionately important role in word meaning, the unique activations associated with these features as they contribute to nominal kinds and complex nouns underlines their different roles in semantic memory. Relative to the characteristic features of a nominal kind, the diagnostic feature of a nominal kind recruits left dorsolateral prefrontal and right parietal regions. We noted above that right parietal activation may support the coarse coding of diagnostic features that are reliably present in a nominal kind. Dorsolateral prefrontal cortex is associated with modulation of cognitive resources, perhaps by biasing responses towards a particular choice in a top-down manner consistent with the larger context or goal of a decision (Badre et al., 2004; Botvinick et al., 2001; Carter et al., 2000; MacDonald et al., 2000). There may be little dorsolateral prefrontal activation for high-contribution features of complex nouns, from this perspective, since little basis for biasing a decision about description accuracy can be derived from the relatively unreliable occurrence of features in complex nouns. We doubt that maintaining diagnostic features in working memory explains prefrontal activation for diagnostic features (Braver et al., 1997; Cohen et al., 1994) because empirical evidence relates dorsolateral prefrontal activation to the planning needed to manage a difficult task (Barch, Braver, Nystrom, Forman,

& Cohen, 1997; Garavan, Ross, Li, & Stein, 2000; Rowe & Passingham, 2001). Prefrontal activation during semantic memory studies may be attributed to an action feature associated with the use of a TOOL because of its proximity to motor cortex (Cappa et al., 1998; Grabowski et al., 1998; Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995; Perani et al., 1995), but sensory-motor features are less prominent in nominal kinds and the activated region is in multimodal association cortex. Another possible explanation for dorsolateral prefrontal activation during diagnostic features of nominal kinds is that the meaning of a nominal kind is established in a rule-like manner. Previous reports associate rule-based categorization decisions with dorsolateral prefrontal activation (Grossman et al., 2002b; Koenig et al., 2005). In contrast to prefrontal activation for diagnostic features of nominal kinds, inferior frontal activation for high-contribution features of complex nouns may support retrieval of probabilistic feature knowledge from semantic memory (Badre, Poldrack, -Blagoev, Insler, & Wagner, 2005; Thompson-Schill, 2003; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997; Wagner, Pare-Blagoev, Clark, & Poldrack, 2001).

Activation for characteristic features is greater than activation for diagnostic features for nominal kinds. This activation, in ventral temporal cortex, is often associated with the representation of visual features (Joseph, 2001; Martin et al., 2000). Regardless of the basis for this activation, we see no significant recruitment for low-contribution features relative to high-contribution features of a complex noun. While a characteristic feature is distinguished from the diagnostic feature of a nominal kind by their special status, a feature contributes to a complex noun's meaning only in a statistical sense. Low-contribution and high-contribution features thus may be insufficiently distinguished to produce significant activation. The observation of a distinct activation pattern for characteristic features of a nominal kind but not low-contribution features of a complex noun provides additional evidence consistent with the view that there are two routes to word meaning.

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FIGURE 1. ACTIVATIONS FOR COMPLEX NOUNS, NOMINAL KIND NOUNS, AND DIAGNOSTIC/HIGH-CONTRIBUTION FEATURES. Panel A: Activations significantly greater for complex nouns than nominal kind nouns; Panel B: Activations significantly greater for nominal kind nouns than complex nouns; Panel C: Activations significantly greater for diagnostic/high-contribution features than characteristic/low-contribution features.

FIGURE 2. ACTIVATIONS FOR DIAGNOSTIC FEATURES OF NOMINAL KIND NOUNS AND HIGH-CONTRIBUTION FEATURES OF COMPLEX NOUNS. Panel A: Activations significantly greater for diagnostic features than characteristic features of nominal kind nouns; Panel B: Activation significantly greater for high-contribution features than low-contribution features of complex nouns.

TABLE 1

ACTIVATIONS ASSOCIATED WITH DIAGNOSTIC/HIGH-CONTRIBUTION AND CHARACTERISTIC/LOW CONTRIBUTION FEATURES OF COMPLEX AND NOMINAL KIND NOUNS

CONTRAST	ANATOMIC LOCUS (BRODMANN AREA)	COORDINATES	T-SCORE	P-VALUE
		X Y Z		
Complex nouns	Bilateral dorsal anterior cingulate (32/6)	8 14 44	6.20	.01
	Right inferior frontal (6/44)	40 5 29	8.65	.000
	Right inferior frontal (47)	48 12 -1	6.17	.02
Nominal kind nouns	Bilateral dorsal anterior cingulate (32/6)	4 2 48	6.17	.02
	Bilateral medial parietal/occipital (7/31)	0 -60 47	6.05	.02
	Right inferior frontal (6/44)	44 -2 44	8.82	.000
	Right superior temporal (21/22/39)	51 -58 12	7.85	.000
	Left dorsolateral prefrontal (45/46)	-48 31 2	5.89	.04
Complex minus nominal kind nouns	Left superior temporal (22)	-44 -12 -3	6.23	.01
	Right superior temporal (22)	44 -12 -6	8.05	.000
	Bilateral medial parietal (7/31)	0 -63 51	7.05	.003
	Right inferior parietal (39)	51 -57 21	6.37	.01
Diagnostic/high-contribution features	Left thalamus	-16 -15 19	5.83	.04
	Bilateral dorsal anterior cingulate (32/6)	4 29 39	7.29	.001
	Right inferior frontal (6/44)	40 -2 41	8.15	.000
	Right inferior frontal (47)	55 12 -1	6.62	.007
	Right inferior parietal (39)	32 -56 54	6.86	.004
	Right thalamus	12 -7 19	6.20	.01
	Right occipital (17/18)	16 -93 5	6.13	.02
Characteristic/low-contribution features	Bilateral thalamus	12 -7 11	5.83	.04
	Bilateral dorsal anterior cingulate (32/6)	4 21 39	5.79	.05
	NO SIGNIFICANT ACTIVATIONS			
Characteristic/low-contribution minus diagnostic/high-contribution features				

TABLE 2
ACTIVATIONS ASSOCIATED WITH HIGH-CONTRIBUTION AND LOW-CONTRIBUTION FEATURES OF COMPLEX NOUNS AND
DIAGNOSTIC AND CHARACTERISTIC FEATURES OF NOMINAL KIND NOUNS

CONTRAST	ANATOMIC LOCUS (BRODMANN AREA)	COORDINATES			T-SCORE	P-VALUE
		X	Y	Z		
Complex nouns: high-contribution features	Right inferior frontal (6/44)	36	1	26	7.60	.001
	Right inferior frontal (47)	48	19	-1	6.45	.01
	Right inferior parietal (40)	44	-52	43	6.43	.01
	Bilateral thalamus	-12	-11	19	6.78	.005
Complex nouns: low-contribution features	NO SIGNIFICANT ACTIVATIONS					
	Right inferior frontal (6/44)	44	2	44	7.13	.002
	Right superior temporal (22/39)	51	-58	14	6.64	.007
	Right inferior parietal (40/7)	32	-56	54	7.02	.003
Nominal kinds: characteristic features	Right superior temporal (22/39)	55	-57	18	6.29	.01
	Right parietal/occipital (19/7)	20	-56	51	6.21	.01
	Right inferior frontal (47)	44	23	-5	6.17	.02
	NO SIGNIFICANT ACTIVATIONS					
Complex nouns: low-contribution minus high-contribution features	Left dorsolateral prefrontal (9)	-51	13	29	5.81	.05
	Right parietal/occipital (39/7/19)	44	-44	50	5.74	.06
	Right ventral temporal (20)	28	-40	-15	6.06	.02
	NO SIGNIFICANT ACTIVATIONS					