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Neuroanatomically separable effects of imageability and grammatical class during single-word comprehension

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Abstract

The present study characterizes the neural correlates of noun and verb imageability and addresses the question of whether components of the neural network supporting word recognition can be separately modified by variations in grammatical class and imageability. We examined the effect of imageability on BOLD signal during single-word comprehension of nouns and verbs. Subjects made semantic similarity judgments while undergoing functional magnetic resonance imaging (fMRI). Nouns and verbs were matched on imageability, and imageability varied continuously within a grammatical category. We observed three anatomically separable effects: a main effect of grammatical class, a main effect of imageability, and an imageability by grammatical class cross-over interaction. The left superior parietal lobule and a region in the left fusiform responded similarly to increases in noun and verb imageability; the left superior temporal gyrus showed greater activity for verbs than nouns after imageability was matched across grammatical class; and, in both the left middle temporal gyrus and the left inferior frontal lobe, a decrease in noun but not verb imageability resulted in higher BOLD signal. The presence of reliable and anatomically separable main effects of both imageability and grammatical class renders unlikely the hypothesis that previously reported dissociations between nouns and verbs can be dismissed as imageability effects. However, some regions previously thought to respond to grammatical class or imageability instead respond to the interaction of these variables.

Keywords: Grammatical class; Imageability; Verb; Noun; Prefrontal cortex; Temporal lobe; Superior temporal gyrus; Superior parietal lobule; Left inferior frontal gyrus; Middle temporal gyrus; Single-word comprehension; Concreteness

1. Introduction

Words can refer to different classes of semantic information such as objects, actions, events, and qualities. Additionally, words contain representations at the syntactic, phonological, and orthographic levels. An important question is how such lexical distinctions are realized in the neural systems that support language. Answering this question is complicated by the fact that the linguistic and semantic properties of words are frequently correlated. For example, nouns tend to refer to objects and easily bring to mind a visual image. On the other hand, verbs tend to refer to events and actions and are less imageable. In addition to these semantic differences, and in part because of them, verbs and nouns play distinct roles in syntactic structure. This confound has made it difficult to dissociate the effects of semantic variables and grammatical variables on word retrieval. One point of controversy is whether imageability and grammatical class have independent effects on the neural instantiation of words.

The concept of imageability is closely related to concreteness and most concrete words are highly imageable. However, this correlation breaks down for general concrete terms such as “animal,” which are relatively low in imageability. It is generally agreed upon that the meanings of highly imageable words contain some sort of additional semantic information. However, different ideas exist about the nature of this additional semantic information. According

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to Paivio, the meanings of highly imageable words contain perceptual representations, in addition to propositional information, while the meanings of low-imageability words contain only propositional information (Paivio, 1971, 1991; Paivio, Walsh, & Bons, 1994). Alternatively, it has been proposed that the meanings of high-imageability words contain more propositional information relative to low-imageability words, which renders low-imageability words more contextually dependent (Jones, 1985; Kieras, 1978; Martin-Loeches, Hinojosa, Fernandez-Frias, & Rubia, 2001; Schwanenflugel, Harnishfeger, & Stowe, 1988). Despite this theoretical equivocality about imageability, the concept has been an important part of psycholinguistic and now neurolinguistic research.

The imageability of words impacts behavioral and neural measures: nouns with high-imageability ratings are remembered better than nouns with low-imageability ratings in long-term memory experiments (Paivio et al., 1994), elicit shorter lexical decision times (Schwanenflugel et al., 1988), and are easier to read for patients with deep dyslexia (Jones, 1985). Several brain regions that are important for semantic processing, such as the left inferior temporal and parietal cortices, respond to increases in imageability (Berndt, Mitchum, Haendiges, & Sandson, 1997a; Binder, Westbury, McKiernan, Possing, & Medler, 2005; D'Esposito et al., 1997; Fletcher et al., 1995; Jessen et al., 2000; Thompson-Schill, Aguirre, D'Esposito, & Farah, 1999; Whatmough, Verret, Fung, & Chertkow, 2004; Wise et al., 2000). The left lateral temporal and inferior frontal cortices, on the other hand, have been reported to respond to decreases in imageability (Binder et al., 2005; Fiebach & Friederici, 2003; Friederici, Opitz, & von Cramon, 2000; Jessen et al., 2000; Mellet, Tzourio, Denis, & Mazoyer, 1998; Wise et al., 2000). However, more activity for concrete than abstract words was recently reported in the left inferior frontal and middle temporal gyri (Giesbrecht, Camblin, & Swaab, 2004).

Grammatical class has generally been overlooked in studies of imageability. Most studies of imageability have used only nouns (Binder et al., 2005; Jessen et al., 2000), while in some cases the grammatical class of the stimuli is not reported (Giesbrecht et al., 2004). It is possible that seemingly incompatible results e.g., (Giesbrecht et al., 2004) reflect the selection of stimuli from different grammatical categories. However, imageability effects are frequently described as applying to words in general. An exception is an experiment by Perani and colleagues (1999) that used a lexical decision task to probe the neural representations of abstract and concrete verbs and nouns. In this study, concrete words did not activate any regions more than abstract words. Collapsing over grammatical class, abstract words elicited greater activity in several regions including bilateral inferior frontal and left posterior temporal cortices (Perani et al., 1999). Concreteness and grammatical class did not interact in these brain regions. These findings do not address the question of whether positive imageability effects are consistent across nouns and verbs, but support the hypothesis that negative imageability effects do not interact with grammatical class.

However, there is some indirect evidence to the contrary. Grossman and colleagues (2002) measured fMRI activation during pleasantness judgments of either motion or cognition verbs. While imageability was not reported for the items used in this study, in general cognition verbs are less imageable than motion verbs. Consistent with studies of noun imageability, they find greater activity for motion (high-imageability) verbs than for cognition verbs in left ventral temporal–occipital cortex, but greater activity for cognition than motion verbs in the left posterolateral temporal cortex. However, they also reported greater activity for motion verbs in bilateral prefrontal cortex, a finding that is not consistent with most studies of noun imageability (Friederici, Meyer, & von Cramon, 2000; Mellet et al., 1998; Perani et al., 1999; Wise et al., 2000). This discrepancy could reflect an interaction between imageability and grammatical class.

Further evidence that imageability effects may not be similar across grammatical classes comes from a study which compared the processing of nouns and function words (e.g., for, but, the). A grammatical class by imageability interaction was observed in both left frontal and temporal cortices (Friederici et al., 2000). With few studies on the topic, and several contradictory findings, neural correlates of verb imageability remain unknown.

Whether and how imageability interacts with grammatical class also bears on a central question in the cognitive neuroscience of language: is the grammatical information associated with nouns and verbs represented in different neuroanatomical regions? There is conflicting evidence in the literature: numerous patient studies have shown that damage to sub-regions of the left inferior frontal, or lateral temporal cortices can lead to noun and verb dissociations in production performance. Damage to the left inferior frontal cortex is most frequently associated with verb deficits (but see Shapiro & Caramazza, 2003a). Although verb deficits are also found in posterior-type aphasia (Berndt, Mitchum, Haendiges, & Sandson, 1997b; Druks, 2002; Shapiro & Caramazza, 2003b; Shapiro & Levine, 1990), these patients more typically have disproportionate deficits in noun production (Daniele, Giustolisi, Silveri, Colosimo, & Gainotti, 1994). Based on these findings several authors hypothesize that the grammatical aspects of verbs and nouns are represented by different brain regions (Berndt et al., 1997b; Bird, Howard, & Franklin, 2003; Caramazza & Hillis, 1991).

Alternatively, dissociations between nouns and verbs may result from semantic variables, such as imageability, that are confounded with grammatical class (Bird, Howard, & Franklin, 2000; Pulvermuller, Mohr, & Schleichert, 1999). It has been proposed that imageability can account for most (if not all) reported grammatical class dissociations (Bird, Franklin, & Howard, 2002; Bird et al., 2003). According to this hypothesis, low-imageability and high-imageability words are neurally dissociable, and apparent dissociations between nouns and verbs result from the lower imageability of verbs.

The imageability account of grammatical class dissociations is made plausible by the fact that the left posterolateral temporal and inferior frontal regions have been implicated in the neural instantiations of both grammatical class and imageability differences. For example, the left inferior frontal gyrus has been reported to respond more to abstract than concrete words (Perani et al., 1999), and more to verbs than nouns when conjugated words were used (Tyler, Bright, Fletcher, & Stamatakis, 2004). According to the imageability account of grammatical class effects, the left frontotemporal network is engaged to a greater extent for verbs and function words as a result of their lower imageability, not their grammatical class. Damage to this network results in a deficit for low-imageability words, which disproportionately affects verbs and function words.

The extent to which verb–noun dissociations can be entirely accounted for by imageability differences remains unclear. Conflicting data exist in the literature: several studies reported that patients with grammatical class dissociations no longer show these effects when imageability is matched for nouns and verbs (Bird et al., 2002, 2003). Conversely, others have identified patients with grammatical class dissociations that persist even when imageability is controlled for (Luzzatti et al., 2002). Cases of modality specific, category-specific grammatical class effects also suggest that semantic differences, such as imageability, cannot account for all grammatical category dissociations in patient performance (Caramazza & Hillis, 1991; Rapp & Caramazza, 1998, 2002). Based on these findings, it has been argued that the effects of imageability and grammatical class on patient performance are independent (Berndt, Haendiges, Burton, & Mitchum, 2002; Luzzatti et al., 2002).

In contrast to the imageability account of grammatical class effects, the hypothesis that imageability and grammatical class effects are independent predicts that some brain regions respond to imageability and not grammatical class, while others show the reverse pattern. Based on parsimony, the absence of such anatomically dissociable effects of imageability and grammatical class would favor the imageability account. If imageability can account for the data, no grammatical category dissociations need be postulated. Notably however, the presence of a region that responds to imageability and grammatical class would not necessarily support the imageability account. Such a region may respond to elements of task complexity, which may be independently affected by grammatical class and imageability.

Neuroimaging studies have thus far been unable to determine whether grammatical class and imageability affect activity in different brain regions. Very few studies have controlled for and/or manipulated both imageability and grammatical class within the same experiment. To date, the only neuroimaging study to examine the interaction of grammatical class and concreteness/imageability appears to support the independence of these variables (Perani et al., 1999). Comparable grammatical class effects for both concrete and abstract words were observed in the left inferior frontal and lateral temporal cortices (Perani et al., 1999).

However, Tyler and colleagues (2004) pointed out that the words used by Perani et al. (1999) were conjugated, and therefore required morphosyntactic processing. Because morphosyntactic processing of verbs may be different from that of nouns, greater activity for verbs than nouns may not reflect the automatic retrieval of grammatical information associated with verbs, but rather may be due to morphosyntactic processing (Tyler et al., 2004). Additionally, imageability ratings were not reported by Perani et al. (1999); thus it is possible that the verb category was, on average, lower in imageability then the noun category. Apparent grammatical class effects could therefore still be attributed to the lower imageability of verbs. There is some evidence that when imageability is controlled, and no morphosyntactic processing is required, no grammatical class effect is present (Tyler et al., 2004; Tyler, Russell, Fadili, & Moss, 2001).

The current study addresses whether imageability and grammatical class affect activity in different neural populations by continuously varying imageability across items while also manipulating grammatical class (nouns vs. verbs). We focus on comprehension of uninflected verbs and nouns outside of sentence context.

2. Materials and methods

2.1. Materials

We obtained imageability ratings for 500 words (nouns and verbs) from 75 participants who completed a rating survey posted on a website. We chose stimuli that were highly biased to be interpreted as either nouns or verbs based on usage in the English Language: stimuli used as verbs occur at least 10 times more frequently as verb than as nouns, and stimuli used as nouns occur at least 10 times more frequently as nouns (Francis & Kucera, 1982). To further induce the intended interpretation, as verbs and nouns, respectively, verbs were preceded by "to" and nouns by "the." The 500 words were divided into subsets of 100; each subset was rated by at least 20 participants (on average each word was rated by 23 participants, $SD = 1.59$, range 21–25). Subjects were instructed to rate each word on its imageability on a scale from 1 to 7, where 1 is least imageable and 7 is most imageable. Variability across subjects was comparable for nouns and verbs, across almost the full range of ratings for both nouns and verbs. As can be seen in Fig. 1, the 95% confidence interval for each rating was generally within 1.2 points on a 7 point scale. Based on this pilot study 199 words were chosen, 100 verbs (V) and 99 nouns (N), these were matched on imageability across grammatical categories.[1] Mean noun imageability (NI) was

[1] The intent was to choose 100 verbs and 100 nouns, however subsequent to data collection, one noun was found to repeat in the stimulus set.

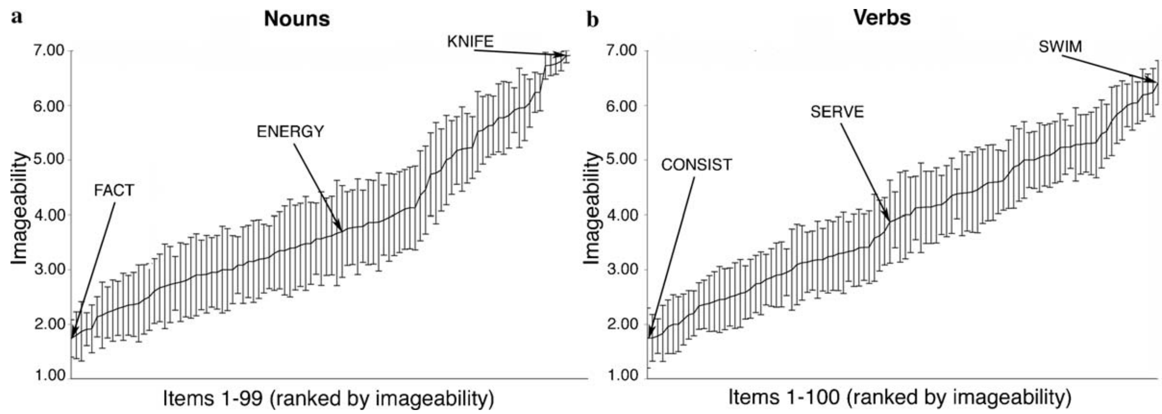

Fig. 1. Imageability ratings for target nouns (a) and target verbs (b) used in the word comprehension task. Error bars depict the 95% confidence interval around the imageability rating for each word. Superimposed on the graph are examples of low-, medium-, and high-imageability words.

3.95 ($SD = 1.45$, range 1.74–7), and mean verb imageability (VI) was 3.91 ($SD = 1.27$, range 1.75–6.42). Nouns and verbs were also matched on length in letters: mean length was 5.8 letters ($SD = 1.5$) for both nouns and verbs. Mean noun frequency (as a noun) was 204 ($SD = 131.9$), and mean verb frequency (as a verb) was 200 ($SD = 166$) (Francis & Kucera, 1982). The verb and noun stimuli were not significantly different on any of the above measures ($t < 1$ in all comparisons). There was no correlation between imageability and frequency for either nouns or verbs ($t < 1$), and there was a negative correlation between imageability and length for both nouns [$R^2 = .05$, $t(98) = -2.34$, $p < .05$] and verbs [$R^2 = .16$, $t(99) = -4.38$, $p < .001$].

2.2. Participants

Thirteen subjects (8 females and 5 males) participated in the experiment. Their mean age was 25.75 (range 20–31). All participants were right handed and had spoken only English until at least the age of 5. None of the participants suffered from psychiatric or neurological disorders or had ever sustained head injury. All subjects gave informed consent to participate in the study and were paid $15 an hour for taking part in the experiment. Subjects came into the laboratory one day before the fMRI scan for a prescreening (to make sure they could safely participate in an fMRI study) and to become familiarized with the task through a five-minute practice session.

2.3. Procedure

The experiment consisted of 300 trials (200 word trials and 100 non-word trials). On each word trial, participants saw a single word followed by a pair of words. The task was to decide which pair member was most similar in meaning to the immediately preceding single word. All stimuli were presented visually on a black screen. Each run contained 10 non-word and 20 word trials. Stimuli appeared in a pseudo random order with no more than four trials of the same type in a row (word or non-word trials). Across subjects, the order of stimuli within a run and run order were randomized.

Each trial lasted 15 s and consisted of a target-word, a word pair and a jittered inter trial interval (ITI). Subjects were instructed to press the left or the right button to indicate which of the pair words was most similar in meaning to the target-word. The word pair followed the target-word, so that participants could not know what similarity judgment they would be making while reading the target-word. On each word trial, a target-word appeared for 2, 4 or 6 s. After the target-word left the screen, a pair of words appeared for 2 s or until the subject made a response. If the subject made a response before the 2 s had elapsed the word pair was replaced by a crosshair for the remainder of the 2-s period. The word pair was followed by a jittered inter trial interval (ITI) that lasted 7, 9 or 11 s. The length of the ITI was yoked to the length of the target-word presentation such that the entire trial duration was always 15 s. During the ITI, a crosshair appeared in the center of the screen. Subjects were instructed to fixate on the crosshair during the ITI. The inter trial interval fixation was used as the baseline for purposes of data analysis (see Fig. 2 for trial structure).

Non-word trials (which were randomly interspersed through out the experiment) were similar in event sequence to the word trials. The non-words were matched to the word stimuli on length in letters (mean = 5.8, $SD = 1.5$) and, like the word stimuli, were preceded by "to" or "the." The non-words appeared in yellow on a black background. The stimuli were presented in 10 runs of 30 trials each. Prior to the experiment, subjects were instructed that yellow font indicated a non-word trial. On non-word trials, subjects were instructed to select the pair member that was identical to the initial non-word target.

2.4. Data acquisition

Structural and functional data were collected on a 3.0 Tesla Siemens Trio scanner using a transmit/receive gradient head coil. High-resolution T1-weighted structural

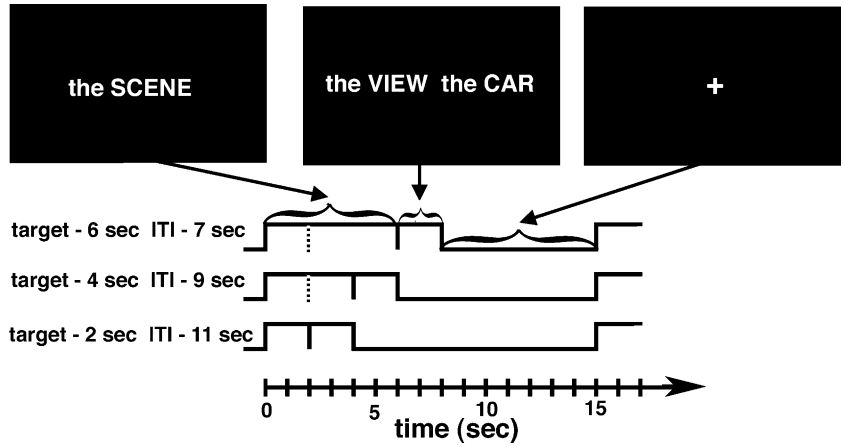

Fig. 2. Trial structure of the word triplet task. Subjects saw the target for 6, 4 or 2 s. This time period was modeled as a 2 s stimulus and a 0, 2 or 4 s ITI (indicated by the dashed line). The target was followed by a word pair (presented for 2 s). Participants pressed the left or right button to indicate which of the pair members was most similar in meaning to the target-word. The word-pair was followed by an inter stimulus interval (ITI) which was 7, 9 or 11 s long.

images were collected in 160 axial slices and near isotropic voxels (0.9766 mm × 0.9766 mm × 1.0000 mm; TR = 1620 ms, TE = 3 ms, TI = 950 ms). Functional, blood oxygenation level dependent (BOLD), echoplanar data were acquired in 3 mm isotropic voxels (TR = 3000, TE = 30). BOLD data were acquired in 42 axial slices, in an interleaved fashion with 64 × 64 in plane resolution using a prospective motion correction (PACE) sequence. The functional data were collected in 10 runs of 7 min and 14 s each. The first 24 s of each run consisted of a "dummy" gradient and radiofrequency pulse to allow for steady state magnetization.

2.5. Image processing

Off-line data analysis was performed using VoxBo (www.voxbo.org) and SPM2 (SPM2 http://www.fil.ion.ucl.ac.uk/) software. Using VoxBo, data were sinc interpolated in time to correct for the slice acquisition sequence. Data were then motion corrected with a six parameter least squares rigid body realignment routine using the first functional image as a reference. The data were smoothed with an 8 × 8 × 8 mm full width at half maximum Gaussian smoothing kernel. Data were then normalized in SPM2 to a standard template, in Montreal Neurological Institute (MNI) space. Normalization maintained 3 mm isotropic voxels and used 4th degree B-spline interpolation.

2.6. Data analysis

2.6.1. First level model

The modified (for serially correlated error terms) general linear model was used to analyze BOLD activity of each subject as a function of condition, on each trial (Worsley & Friston, 1995; Zarahn, Aguirre, & D'Esposito, 1997a). fMRI signal change was modeled by creating covariates for each event type including non-word target-word, noun target-word, verb target-word, non-word pair, noun pair, verb pair, and baseline. Events were modeled as a 2 s target-word, 0, 2 or 4 s ITI, a 2 s word pair, followed by a 7, 9 or 11 s ITI. The time period between the presentation of the target-word and the presentation of the word pair was modeled as ITI, even though the target-word stayed on the screen during this time. The target-word was maintained on the screen so that subjects would not assume the strategy of intentionally committing the target-word to memory upon its presentation. To account for the effects of having the stimulus on the screen for 2, 4 or 6 s, a covariate was included to model the amount of time that each target-word was presented. Neural activity was modeled as a brief impulse at stimulus onset (Zarahn et al., 1997a). Two additional covariates of interest were used to model the imageability of target-word nouns and target-word verbs separately; each of these was mean centered. Covariates of interest were convolved with a standard hemodynamic response function (HRF).

Nuisance covariates for effects of scan, global signal, and motion were included. Time series data were subjected to a high-pass (.0177 Hz) filter, and serial correlation of error terms was modeled as previously described (Zarahn, Aguirre, & D'Esposito, 1997b).

2.6.2. Second level region of interests (ROI) and whole-brain analyses

BOLD signal differences between words and non-words, nouns and verbs, imageability, and the interaction of these effects were evaluated through second level (random effects) analyses. Second level analyses were performed on the β-values obtained from the first level analysis, after these were scaled by the error term to account for scaling effects in fMRI time series (hereafter, scaled β-values will be referred to as β's.) All effects were tested using multiple regression analysis, with subject as a random effect. For whole-brain analyses, the false positive rate was controlled ($\alpha < .05$ corrected for multiple comparisons with a minimum cluster size of 15 voxels) by performing 2000 Monte-Carlo permutation tests on the data (Nichols & Holmes, 2002). In anatomical ROI analyses, β-values were calculated for a single, spatially averaged time series for each ROI.

ROI analyses were conducted to directly test hypotheses about the role of the left prefrontal and posterolateral temporal cortices in grammatical class effects. Several authors have proposed that the left prefrontal (Perani et al., 1999; Shapiro & Caramazza, 2003a) and posterolateral temporal cortices encode verb specific information (Davis, Meunier, & Marslen-Wilson, 2004; Kable, Lease-Spellmeyer, & Chatterjee, 2002). To test for grammatical class effects in these regions, seven ROI's were created based on previous neuroimaging findings.

In the left frontal lobe, Perani et al. (1999) reported verb specific activation during a lexical decision task. Based on these results, two ROI's were created, one on the border of the middle frontal and left inferior frontal gyri (LMFG/LIFG BA45/46; $X=-36$, $Y=30$, $Z=20$), and a second in the left middle frontal gyrus (LMFG BA46; $X=-28$, $Y=28$, $Z=28$). Additionally, Tyler and colleagues (2004) reported greater activity for verbs than nouns during a morphosyntactic task. Based on this finding, three ROI's were created in the left inferior frontal gyrus (LIFG): LIFG BA44 ($X=-50$, $Y=16$, $Z=12$), LIFG BA47ant ($X=-38$, $Y=22$, $Z=6$), and LIFG BA45 ($X=-46$, $Y=22$, $Z=6$). In left posterolateral temporal cortices, Davis et al. (2004) reported greater activity for verbs than nouns during a one-back synonym-monitoring task. Two anatomical ROI were created based on these findings, one in the left middle temporal gyrus (LMTG BA37, $X=-54$, $Y=-48$, $Z=-6$) and a second in the posterior aspect of the left superior temporal gyrus (LSTG, BA42/40, $X=-54$, $Y=-36$, $Z=21$).[2]

Two ROI were created to examine whether the left fusiform and left prefrontal cortex (LPFC), which have previous been shown to respond to noun imageability, respond similarly to verb imageability. Increases in noun imageability have been consistently shown to result in increased activity in the inferior temporal cortices, and the left fusiform in particular (e.g., D'Esposito et al., 1997; Wise et al., 2000). This region is believed to represent visual semantic information, and has also been hypothesized to represent object concepts (Tyler et al., 2004). To test the hypothesis that the left fusiform is important for representing visual information relevant to objects and events, an ROI was created based on previous findings. Wise et al. (2000) reported a region in the left fusiform that was more active for high-imageability than low-imageability nouns when subjects passively listened to, read, or made semantic decisions based on words. Based on the findings of Wise et al. (2000) an anatomical ROI was created in the left fusiform (LFus; $X=-31$, $Y=-40$, $Z=-24$).

In contrast, several studies have reported negative imageability effects in the left inferior frontal cortex (e.g., Binder et al., 2005; Friederici et al., 2000; Perani et al., 1999). For example, Perani and colleagues (1999) reported greater activity for low-imageability than high-imageability words in the left inferior frontal gyrus during a lexical decision task. To test whether left inferior frontal imageability effects are consistent across grammatical categories. We created an ROI in the LIFG (LIFG BA47post, $X=-44$, $Y=14$, $Z=-4$) (Perani et al., 1999).

All nine anatomical ROI's were created by growing spheres of 19 voxels centered on the reported peaks of activation (converted to MNI if reported in Talairach). The resulting ROI's were overlaid onto random effects models of grammatical class and imageability. To assess significance, time series were averaging over the entire ROI: the results are summarized in Table 2.

Following the anatomical ROI results, we report whole-brain analyses for imageability, grammatical class, and the interaction of the two.

3. Results

3.1. Behavioral results

Behavioral data were only available for six of the 13 subjects (all comparisons were evaluated using the within-subject Wilcoxon Sign Rank Test due to this small sample). Participants were significantly more accurate ($z=-10.5$, $p<.05$) and faster ($z=-10.5$, $p<.05$) to make a decision for non-word (99.8 ± .5%, 684 ± 124 ms) than word trials (96.8 ± 1.6%, 1117 ± 157 ms). There was no significant difference between noun and verb responses in either accuracy (nouns 97 ± 1%, verbs 97 ± 3%) or reaction time (nouns 1102 ± 185 ms, verbs 1131 ± 137 ms) ($p>.40$). To evaluate the effect of imageability on reaction time we first regressed reaction time by target-word imageability for each subject. The resulting effect estimates of imageability were used as the dependent variable in a subjectwise Wilcoxon Sign-Rank test. As the imageability of the target-word increased, response times decreased slightly across participants (average $R^2=.009$, average effects estimate $=-17$ ms, $z=-10.5$, $p<.05$). This effect was significant by item [$R^2=.023$, $t(198)=-2.16$, $p<.05$]. The imageability by grammatical class interaction was not significant ($p>.25$).

3.2. Words compared to non-words

Prior to assessing grammatical class and imageability effects, we examined the Words–Non-words contrast to establish that the current task activates regions that are classically involved in word comprehension. Word–Non-words results are summarized in Table 1 and Fig. 3. Robust activation was found in regions typically activated more for words than non-words, including the left prefrontal and posterolateral temporal cortices.

3.3. Anatomical region of interest analyses (Table 2)

3.3.1. Imageability collapsed across grammatical class

There was a positive effect of imageability on BOLD signal in the LFus ROI [$t(1,12)=2.68$, $p<.05$]. No ROI's

[2] Davis et al. (2004) refer to this region as the superior temporal sulcus. However, based on the coordinates and the figure in Davis et al. (2004), this region lies near the sylvian fissure and is more appropriately described as the posterior aspect of the superior temporal gyrus.

Table 1
Results for whole-brain words vs. non-words contrast

Contrast	Brain region (Brodmann's area)	Peak voxel *t*-value	Cluster size (cm^3)	*X*	*Y*	*Z*
Words > Non-words	Left middle and superior temporal gyri (37/21/22)	14.53	48.9	−57	−48	0
Words > Non-words	Left inferior frontal and middle frontal gyri (47/45/46)	13.82	189	−48	33	3
Words > Non-words	Right and left medial superior frontal gyrus (6/8)	11	111	3	21	54
Words > Non-words	Right posterior cingulate and occipital lobe (30/31/18)	10.86	30.3	27	−66	9
Words > Non-words	Left lingual gyrus and cuneus (17)	8.37	41.4	−15	−90	0
Words > Non-words	Right sublobar/insula (13)	5.74	9.6	39	15	0
Non-words > Words	Left inferior parietal lobule and postcent ral gyrus (40)	11.25	61.2	−60	−30	36
Non-words > Words	Left middle and superior frontal gyri (9)	9.88	20.7	−39	33	39
Non-words > Words	Right precuneus (7)	9.6	27	9	−54	42
Non-words > Words	Left inferior temporal gyrus (20)	9.05	11.1	−60	−24	−24
Non-words > Words	Left inferior parietal lobule and postcentral gyrus (40/2/1)	8.8	33.9	−60	−30	39
Non-words > Words	Right claustrum	8.67	7.2	33	−12	9
Non-words > Words	Right superior frontal gyrus (8)	7.44	33.9	15	30	57
Non-words > Words	Right inferior parietal lobule (40)	7.43	61.5	45	−66	48
Non-words > Words	Left middle occipital gyrus (37)	7.33	7.5	−45	−66	−9
Non-words > Words	Left uncus/amygdala	7.27	6	−24	−3	−24
Non-words > Words	Left precentral gyrus (6)	6.57	11.7	−54	−6	6

Note. Peaks of activation which reached significance at the $p < .05$ lever corrected for multiple comparisons with at least 15 contiguous voxels.

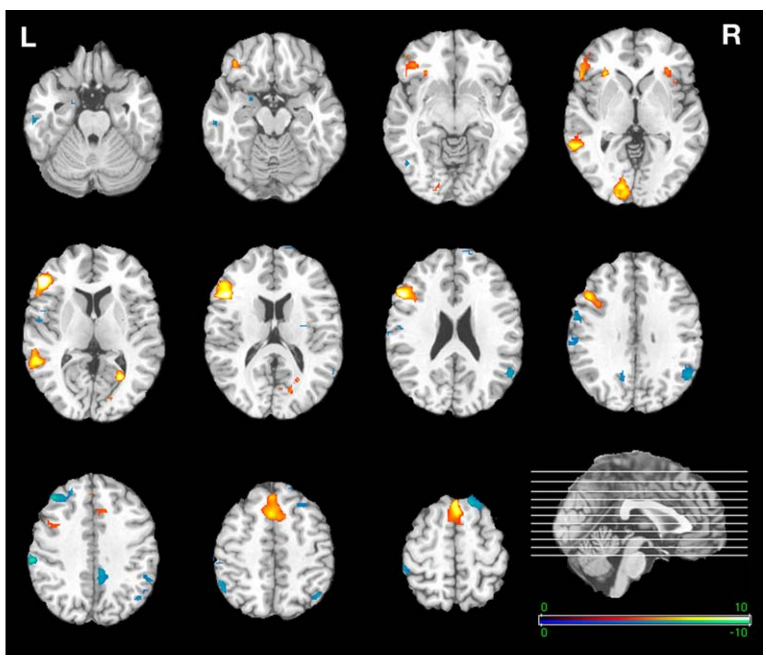

Fig. 3. Results for Words–Non-words contrast. Regions that responded differently to words and non-words, based on a whole-brain random effects analysis overlaid on axial slices of a standard normalized structural image. Regions that responded more to words than non-words are displayed in warm colors, regions that respond more to non-words than words are displayed in cool colors. The *t*-map is thresholded at $p < .05$ corrected for multiple comparisons with at least 15 contiguous voxels.

responded significantly to decreases in imageability collapsing across grammatical class.

3.3.2. Grammatical class effects

In contrast to the findings of Perani et al. (1999), the LMFG/LIFG BA45/46 ROI [$t(12) = -3.79$ $p < .01$] responded more to nouns than verbs in the present study. None of the left inferior frontal gyrus anatomical ROI's responded more to verbs than nouns. The LSTG BA42/40 ROI showed significantly more activity for verbs than nouns [$t(12) = 4.80$, $p < .001$] (Fig. 4). There were no grammatical class effects in the middle temporal gyrus.

3.3.3. Grammatical class and imageability interaction

There was a significant grammatical class by imageability interaction in LIFG BA44 [$t(1,12) = -2.17$, $p < .05$] as well as the LMTG BA37 [$t(12) = -2.29$, $p < .05$] and LSTG BA42/40 [$t(1,12) = -1.93$, $p < .05$] anatomical ROI's. For the three ROI's that showed a grammatical class by imageability interaction, we went on to test noun and verb imageability separately. A decrease in noun imageability was

Table 2
Results for the anatomical region of interest analysis for grammatical class, imageability, and grammatical class by imageability interaction contrasts

Previous finding (source)	Region of interest	Contrasts (t-values)				
		Verb > Noun	Imageability	Interaction	Noun imageability	Verb imageability
Verbs > Nouns						
(Perani et al., 1999)	LMFG[b]/LIFG[a]BA45,46	**−3.79****	−.68	−.56	—	—
(Perani et al., 1999)	LMFG BA46	.19	−.69	**1.87***	−1.74†	.70
(Tyler et al., 2004)	LIFG BA44	1.1	−1.68	**2.17***	**−2.59***	−.16
(Tyler et al., 2004)	LIFG BA47ant	.5	−.1	1.17	—	—
(Tyler et al., 2004)	LIFG BA45	.3	−.29	1.35†	—	—
(Davis et al., 2004)	LMTG[c] BA37	−.6	.78	**2.29***	−1.37†	1.58†
(Davis et al., 2004)	LSTG[d]	**4.8*****	.77	**1.93***	−1.53†	1.79†
−Imageability						
(Perani et al., 1999)	LIFG BA47post	.43	−.44	**−3.06****	**−2.53***	1.86†
+Noun imageability						
(Wise et al., 2000)	LFus[e]	−1.86†	**2.68***	−.48	—	—

Note. Regions of interest were created by growing spheres 19 voxels in volume around peaks of activation reported by the above listed studies. When peaks of activation were reported in Talairarch coordinates they were first converted to MNI space. Significant t-values appear in bold. High-imageability nouns greater than low-imageability nouns.
[a] Left middle frontal gyrus.
[b] Left inferior frontal gyrus.
[c] Left middle temporal gyrus.
[d] Left superior temporal gyrus.
[e] Left fusiform gyrus (see footnote 2).
* $p < .05$.
** $p < .01$.
*** $p < .001$.
† $.05 \leqslant p \leqslant .10$.

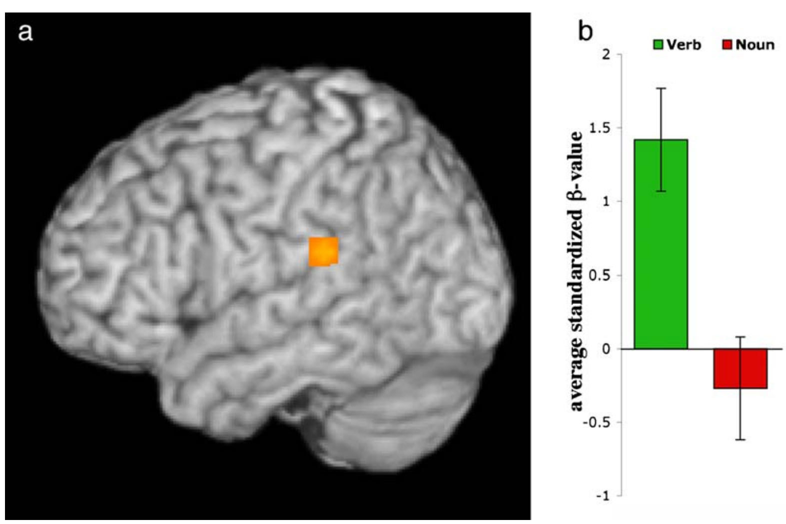

Fig. 4. Results for Verbs–Nouns contrast in the LSTG anatomical ROI (19 voxels in volume and centered on the coordinates reported by Davis et al. (2004) for a verb–noun contrast, $X = -54$, $Y = -36$, $Z = 21$). The ROI is displayed on a 3-D rendered, normalized template of the left hemisphere (a). Average standardized β-value for verbs minus baseline contrast (green) and nouns minus baseline contrast (red). Error bars reflect standard error of the difference (within-subject contrast) between verbs and nouns (b).

associated with an increase in activation in the LIFG BA44 ROI [$t(1,12) = -2.5$, $p < .05$].

3.4. Whole-brain analyses (Table 3, Fig. 5)

3.4.1. Imageability collapsed across grammatical class (Fig. 5a)

Three regions showed increases in activity as imageability increased: a region in the left precuneus and superior parietal lobule (BA19/7, $X = -27$, $Y = -78$, $Z = 39$); a region in the left superior frontal gyrus (BA8, $X = -21$, $Y = 18$, $Z = 54$), and a region in the right posterior middle temporal gyrus (BA39, $X = 45$, $Y = -69$, $Z = 24$). As imageability decreased there was an increase in activity in the left middle occipital gyrus (BA18, $X = -30$, $Y = -99$, $Z = -3$) and right lingual gyrus (BA17, $X = 15$, $Y = -90$, $Z = -3$). These results are based on the critical t-value derived from 2000 Monte-Carlo permutation tests for the imageability

Table 3
Results of whole-brain analysis for the grammatical class/imageability and grammatical class by imageability interaction contrasts

Contrast	Brain region (Brodmann's area)	Peak voxel t-value	Cluster size (cm^3)
Verbs > Nouns	Left posterior cingulate (BA23)	6.75*	5.4
Verbs > Nouns	Left superior temporal gyrus (BA41/13)	4.78†	4.5
Nouns > Verbs	Left inferior temporal gyrus (BA20)	6.31†	4.5
+Imageability	Left superior frontal gyrus (BA8)	6.31*	8.1
+Imageability	Left precuneus and superior parietal lobule (BA19/7)	8.38*	44.7
+Imageability	Right posterior middle temporal gyrus (BA39)	6.31*	5.1
−Imageability	Left middle occipital gyrus (BA18)	5.85*	10.8
−Imageability	Right lingual gyrus (BA17)	6.4*	8.7
Interaction	Left middle temporal gyrus (BA22)	5.1*	5.6
Interaction	Left superior temporal/inferior frontal gyri (BA38/47)	7.5*	5.8

* $p < .05$.
† $p = .065$.

contrast [$t(1,12) = 4.12$, $p < .05$ corrected for multiple comparisons].

3.4.2. Grammatical class (Fig. 5b)

At a critical $t(1,12) = 4.18$, $p < .05$ (corrected for multiple comparisons), there was greater activity for verbs than nouns in the left posterior cingulate gyrus ($X = -9$, $Y = -36$, $Z = 21$). A region in the left, posterior, superior temporal gyrus (LSTG, BA22/42, $X = -57$, $Y = -39$, $Z = 15$) just failed to reach significance for the verbs–noun contrast with a $t(1,12) = 4.12$, $p = .065$. At the threshold of $t(1,12) = 4.12$, $p = .065$ there was also region in the left inferior temporal gyrus (LITG, BA20) ($X = -57$, $Y = -30$, $Z = -21$), which showed greater activity for nouns than verbs. No other regions showed grammatical class effects at this threshold.

3.4.3. Verb and noun imageability interaction (Fig. 5c)

Two regions showed a significant interaction between imageability and grammatical class, a region in the anterior LSTG/LIFG (BA38/47, $X = -54$, $Y = 15$, $Z = -6$) and a region in the LMTG (BA38, $X = -60$, $Y = -51$, $Z = 0$) [$t(1,12) = 4.08$, $p < .05$, corrected for multiple comparisons].

4. Discussion

4.1. Common imageability effects

Activity in the left superior parietal lobule, right posterior middle temporal gyrus, left superior frontal gyrus, and the left fusiform gyrus increased as imageability for nouns and verbs increased (Fig. 4a). The ventral temporal cortices are thought to represent visual semantic information (D'Esposito et al., 1997; Ishai, Ungerleider, & Haxby, 2000; Thompson-Schill et al., 1999), and activity in the left fusiform gyrus has previously been reported to respond to increases in noun imageability (D'Esposito et al., 1997; Fletcher et al., 1995; Fletcher & MacWhinney, 1995; Price, 2000; Wise et al., 2000). The present findings demonstrate that this imageability effect is similar for verbs, suggesting that visual semantic information also plays a role in the semantics of imageable verbs that refer to events and actions.

Increased activity in both the left superior parietal lobule and superior frontal gyrus has previously been reported while subjects viewed grey squares and simultaneously generated visual images from long term memory, as compared to grey square viewing alone. In contrast to activity in the ventral temporal cortex, activity in these regions was not content specific. Based on these findings the authors argued that the superior frontal and parietal cortices are important in retrieving and maintaining visual semantic information, which is stored in the inferior temporal cortex (Ishai et al., 2000). The present findings suggest that the left superior parietal lobule and frontal gyrus are engaged during word reading in the absence of explicit instructions to generate imagery.

The only regions that showed effects of imageability decreases for both nouns and verbs were the right cuneus and lingual gyrus (BA17, BA19). The presence of this activation is very likely due to the negative correlation between word imageability and word length [$R^2 = .10$, $t(197) = -4.79$, $p < .001$], rather than decreases of imageability per se. Both of these regions have previously been shown to respond positively to increases in word length (Tyler et al., 2004).

Notably, there was no main effect of imageability on left inferior frontal activity, either in the ROI or in the whole-brain analyses. This is consistent with the assertion that activity in the LIFG is not specific to abstract or concrete words, but rather responds to the interaction of stimulus characteristics and task demands (Friederici et al., 2000; Thompson-Schill, Bedny, & Goldberg, 2005).

4.2. Grammatical class effects

The left posterior LSTG has previously been shown to respond more to motion verbs than nouns (Davis et al., 2004; Kable et al., 2002; Wallentin, Lund, Ostergaard, Ostergaard, & Roepstorff, 2005). The present study extends these findings by demonstrating that this effect persists even when imageability is matched across the grammatical classes (Fig. 4).

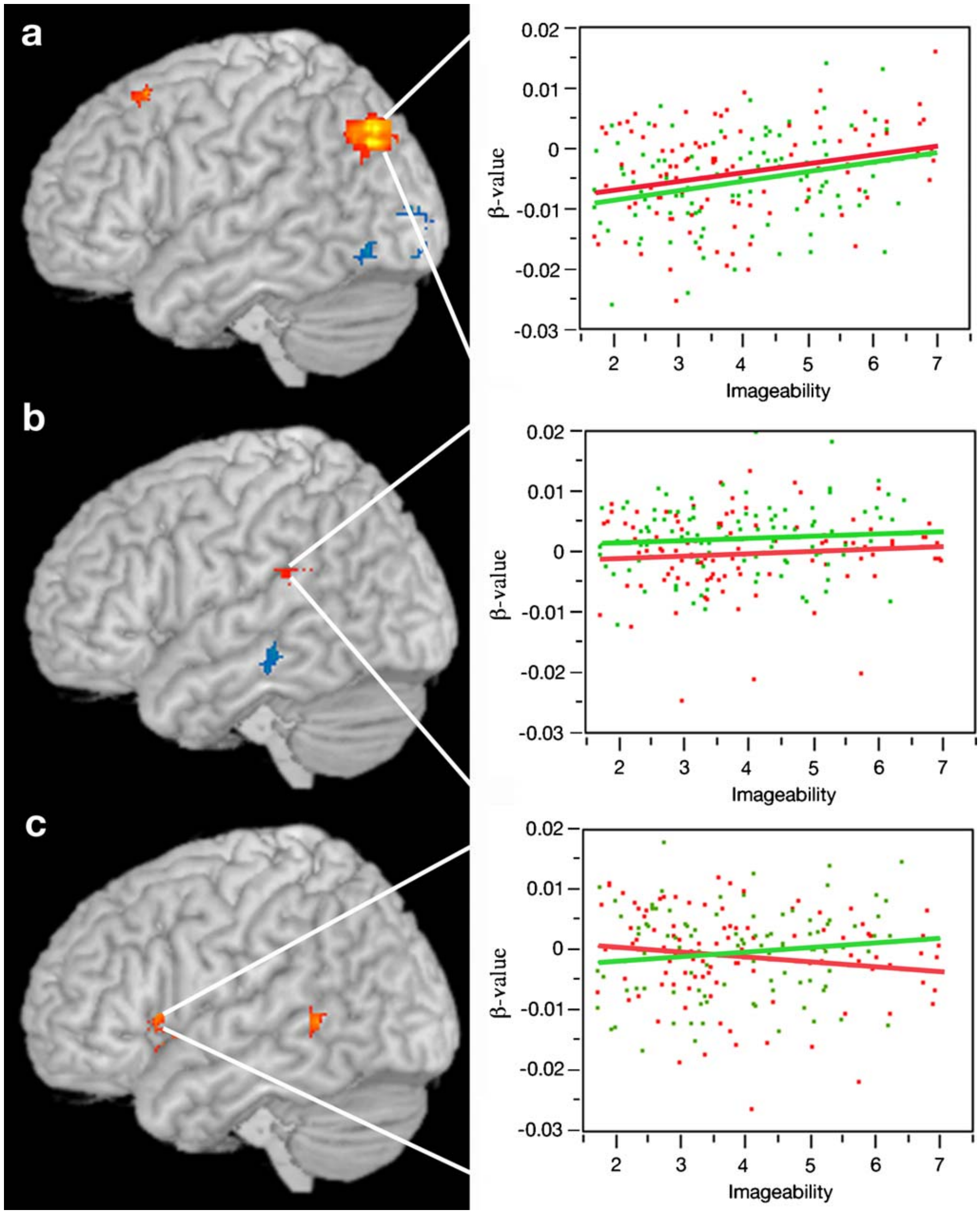

Fig. 5. Examples of regions responding to imageability, grammatical class, and the interaction of grammatical class and imageability. The results of a whole-brain, random effects analysis for the imageability (a), verbs–nouns (b), and interaction (c) contrasts are displayed on a normalized 3-D rendered template of the left hemisphere. The *t*-map for imageability and grammatical class by imageability interaction effects are thresholded at $p < .05$ corrected for multiple comparisons with at least 15 contiguous voxels. The *t*-map for the verbs–nouns contrast is thresholded at $p < .065$ with at least 15 contiguous voxels. To the right of each contrast is a scatter plot of β-values for each word as of function of imageability and grammatical class (verbs in green and nouns in red). Each β-value is derived from the spatially averaged time series across a representative region that showed an effect of imageability, grammatical class or their interaction. Best-fit lines are displayed separately for nouns (red) and verbs (green). (a) Displays activity in the left superior parietal lobule. This region showed a main effect of imageability. (b) Displays activity in the superior temporal gyrus. This region displayed a main effect of grammatical class (more activity for verbs than nouns). (c) Displays activity in a region on the border of the left inferior frontal and superior temporal gyri. This region responded to the interaction of grammatical class and imageability.

While there is now considerable evidence that this region of the LSTG is important for verb processing, its specific contribution is not known. There is some evidence that the posterior LSTG is important for representing the higher order action and motion information, which is an integral part of verb semantics. Davis et al. (2004) showed that activity in this region correlates with subjects' estimates of how much action is associated with a verb. This region is activated during the processing of sound source motion (Warren, Zielinski, Green, Rauschecker, & Griffiths, 2002), motion imagery (Decety et al., 1994), and action naming (Damasio et al., 2001). A proximal region in the superior temporal sulcus (STS) is involved in biological motion representation. Regions within the STS respond to point-light displays of moving humans more than to point light displays of moving objects, and more than to random motion

(Beauchamp, Lee, Haxby, & Martin, 2003). If greater activity in the STG for verbs than nouns reflects action representations, then imageable verbs should activate this region more than non-imageable verbs. To test this hypothesis, we examined the effect of verb imageability on activity in the posterior LSTG region that we identified as more active for verbs than nouns in the whole-brain analysis. This LSTG region did in fact show a positive verb imageability effect [$t(12) = 1.82$, $p = .048$], but did not show a noun imageability effect [$t(12) = -1.27$, $p = .88$]. In combination with previous findings, this suggests that the poster STG is important for representing higher order action and motion information, which is critical to the semantics of concrete verbs.

However, some prior evidence appears to suggest that this LSTG region is involved in retrieving linguistic features, such as syntactic, thematic or pragmatic information. The posterior LSTG becomes more active as syntactic complexity of sentences increases (Just, Carpenter, Keller, Eddy, & Thulborn, 1996), is more active for sentences containing grammatical errors than sentences containing spelling errors (Embick, Marantz, Miyashita, O'Neil, & Sakai, 2000), as well as for sentences that are pragmatically anomalous as compared to sentences which are not. These data in isolation appear to support the notion that the LSTG processes linguistic information. However, in light of the evidence that this region responds to semantic variables such as action content and verb imageability, these results may reflect greater difficulty in arriving at a coherent event model in the linguistically complex conditions. In the linguistically complex conditions discussed above, multiple possible event representations may be activated resulting in greater activity in the posterior LSTG. Seen in this light, these findings are not inconsistent with the hypothesis that the LSTG represents higher order action information.

The posterior cingulate also responded more to verbs than nouns in the present study. Unlike the LSTG, this region did not respond to verb imageability [$t(1,12) = -.33$]. The posterior cingulated is thought to be involved in lexical access, but its exact function in this process is not known (Binder et al., 2003). The function of the posterior cingulate in verb specific processing warrants further research.

While some previous studies have reported more activity for verbs than nouns in the LPFC (Perani et al., 1999; Tyler et al., 2004), we found more activation for nouns than verbs in this region. One possible explanation for this inconsistency across studies is the hypothesis offered by (Shapiro & Caramazza, 2003a): the left inferior frontal gyrus may contain subregions for representing and/or processing information specific to a particular grammatical class. However, in the present study we found that the inferior frontal lobe responded more to nouns than verbs using an anatomical ROI that was previously found by Perani et al. (1999) to respond more verbs than nouns. Consequently, the inconsistency between our findings and those of Perani et al. is not likely solely due to functional heterogeneity within the left inferior frontal lobe.

We hypothesize that two critical differences in paradigm account for the divergence in findings between the present study and studies that report greater activity for verbs than nouns in the LPFC (Perani et al., 1999; Tyler et al., 2004). The nouns used in the present study were relatively low in imageability, because they were matched to a group of verbs. In contrast, previous neuroimaging studies have tended to use concrete nouns and verbs as stimuli. It is possible that in matching our nouns to a group of verbs on imageability, we unintentionally chose nouns that are more abstract in some way that is not captured by the imageability variable. Furthermore, unlike neuroimaging studies that report greater activity in the prefrontal cortex for verbs, words in the present study were not conjugated and thus did not require morphosyntactic processing. All studies of noun and verb comprehension that report greater left prefrontal activity for verbs used conjugated stimuli.

An alternative possibility is that the failure to find verb specific activity in the prefrontal cortex reflects an idiosyncrasy of the present triad task. However, prior evidence renders this an unlikely explanation. Multiple studies of grammatical class effects have employed various version of the triad task (Davis et al., 2004; Kable et al., 2002; Tyler et al., 2004). Of these, only Tyler et al. (2004) found greater activity for verbs than nouns in the LPFC. Tyler et al. (2004) used a paradigm quite similar to the present experiment. Participants saw three words in sequence, when the third word was presented subjects decided whether it was related in meaning to the previous two. While the current study and that of Tyler et al. (2004) used very similar tasks, they differ in that the present study used uninflected nouns and verbs. Tyler and colleagues argued that greater activity for verbs than nouns in the LPFC, reflects the morphological complexity of inflected verbs relative to nouns (Tyler et al., 2004). It therefore seems that the absence of morphosyntactic processing, rather than the current triad task, is most likely responsible for the absence of a verb specific effect in the LPFC. In combination with previous findings, the present data are most consistent with the hypothesis that grammatical class effects in the prefrontal cortex depend on an interaction of stimulus characteristics (e.g., verbs vs. nouns) and task demands (e.g., presence or absence of morphosyntactic processing) (Tyler et al., 2004).

In summary, the LSTG and posterior cingulate were the only regions that responded more to verbs than nouns when imageability was equated and no morphosyntactic processing was required. These regions showed effects of grammatical class that cannot be accounted for by the lower imageability of verbs. In contrast, the present data indicate that differences between verbs and nouns in LPFC and middle temporal gyrus reported in prior studies are not due to the automatic retrieval of verb specific grammatical representations, but rather are mediated by a combination of task demands and stimulus characteristics.

4.3. Imageability and grammatical class interaction

The present study demonstrates that left prefrontal and lateral temporal cortices do not respond similarly to modulation in noun and verb imageability: in several regions including the left inferior frontal and middle temporal gyri there was a significant grammatical class by imageability interaction. While activity increased as imageability decreased for nouns, the opposite was true for verbs. This effect clearly demonstrates that noun imageability effects should not be generalized to verbs without testing the effects of verb imageability directly. Furthermore, given the cross-over interaction between imageability and grammatical class in the inferior frontal and middle temporal gyri (Fig. 5c), it may appear that these regions respond more to verbs than nouns, or vice versa, depending on which part of the imageability distribution is sampled.

One possible explanation of this interaction effect is that it is due to nuisance variables such as frequency and word length. However, subsequent analyses showed that there was no relationship between frequency and imageability in our stimulus set, either for noun or for verbs, and word length was correlated negatively with imageability for both nouns and verbs. Thus, frequency and length do not appear to explain the grammatical class by imageability interaction found in the left posterolateral temporal and inferior frontal cortices.

An intriguing possibility is that the grammatical class by imageability interaction is related to the number of meanings or senses that a word has. In the present stimulus set, there was a grammatical class by imageability interaction when these two variables were used as predictors for sense number ($F = 7.67$, $p < .01$). For verbs, as imageability increased the number of senses increased, while for nouns the trend was in the reverse direction (sense numbers were obtained from the WordNet database, http://wordnet.princeton.edu/) (Miller et al., 2005). The LIFG might respond to semantic conflict that results when a word has many possible meanings or senses. Previous research has shown that this brain region is important for resolving competition during lexical access, and it may become automatically engaged during the comprehension of ambiguous words (Rodd, Davis, & Johnsrude, 2005; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997; Thompson-Schill, D'Esposito, & Kan, 1999). However, sense number is only one possible variable that could explain this interaction. The present study did not manipulate sense number and this "sense-number" hypothesis is only a post hoc explanation, which requires further testing.

5. Conclusions

Our study demonstrates that brain regions involved in word processing can be broadly categorized into four types: those where activity is modulated by word imageability regardless of grammatical class (the left superior parietal lobule and fusiform gyrus); those where activity is modulated by grammatical class, above and beyond imageability (LSTG and posterior cingulate); those where the effects of imageability and grammatical class interact (e.g., LIFG); and those that do not respond to either of these variables or their interaction. These effects are not confounded with word frequency and word length. However, other mediating variables may prove important in understanding the unanticipated interaction between grammatical class and imageability in the LIFG. This study clarifies and extends previous research on word processing by characterizing the neural instantiation of imageability and grammatical class during single-word comprehension.

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