On the basis of neuropsychological and functional imaging evidence, meaning and grammatical class (particularly the verb–noun distinction) have been proposed as organizational principles of linguistic knowledge in the brain. However, previous studies investigating verb and noun processing have been confounded by the presence of systematic correlations between word meaning and grammatical class. In this positron emission tomography study, we investigated implicit word processing using stimuli that allowed the effects of semantic and grammatical properties to be examined independently, without grammatical–semantic confounds. We found that left hemisphere cortical activation during single-word processing was modulated by word meaning, but not by grammatical class. Motor word processing produced significant activation in left precentral gyrus, whereas sensory word processing produced significant activation in left inferior temporal and inferior frontal regions. In contrast to previous studies, there were no effects of grammatical class in left inferior frontal gyrus (IFG). Instead, we found semantic-based differences within left IFG: anterior, but not posterior, left IFG regions responded preferentially to sensory words. These findings demonstrate that the neural substrates of implicit word processing are determined by semantic rather than grammatical properties and suggest that word comprehension involves the activation of modality-specific representations linked to word meaning.

Keywords: grammatical class, language, PET, semantics, word processing

Introduction

Meaning and grammar are universal properties of language, even at the single-word level. Neuropsychological and functional imaging studies have provided evidence of distinct neural substrates for the processing of meaning and grammatical class. Semantic processing of words referring to objects has been linked to multimodal regions in the basal temporal cortex (e.g., Price 1998; Levy and others 2004). More recently, imaging studies have implicated motor and premotor cortices (Hauk and others 2004; Tettamanti and others 2005), and middle temporal regions (Martin and others 1995; Tranel and others 2005) including the visual motion area MT (Damasio and others 2001; Tranel and others 2005), in processing words referring to action or motion. These findings have been taken to support theories in which semantic representation involves distributed networks of motor, sensory, and functional information (Warrington and Shallice 1984; Martin and Chao 2001; Damasio and others 2004). Regarding grammatical class, neuropsychological studies have demonstrated double dissociations between verb-specific impairments, associated with left inferior frontal gyrus (IFG) lesions, and noun-specific impairments, associated with left temporal lobe lesions (Caramazza and Hillis 1991; Damasio and Tranel 1993; Daniele and others 1994; Silveri and Di Betta 1997). In normal subjects, the most consistent evidence of distinct neural substrates for different grammatical classes has come from studies showing verb-specific activation in left IFG (Perani and others 1999; Tyler and others 2004; Shapiro and others 2005), although this has not been a universal finding (Tyler and others 2001).

However, word meaning and grammatical class are highly correlated in most languages: verbs refer to actions or other events, whereas nouns tend to refer to objects and other entities. Thus, studies using verbs referring to actions/events and nouns referring to objects/entities have systematically confounded grammatical class with semantics (Perani and others 1999; Tyler and others 2004), so that verb-specific activation may reflect processing of action-related knowledge (Grezes and Decety 2001) rather than grammatical class. In addition, previous studies showing verb-specific left IFG activation used explicit tasks, such as lexical (Perani and others 1999) or semantic (Tyler and others 2004) decision, or a task in which participants had to produce inflected forms of verbs and nouns in response to a cue (Shapiro and others 2005). Because most languages have more morphologically inflected verb than noun forms (e.g., in English there are at least 4 different forms for verbs and only 2 for nouns), task performance on verbs may place greater demands on selection and decision processes attributed to left IFG (Thompson-Schill and others 1997; Gold and Buckner 2002; Binder and others 2004), so that verb-specific activation may result from an interaction between grammatical class and task demands.

In order to establish whether semantics and grammatical class are independent organizational principles of linguistic knowledge in the brain, these potential confounds must be removed. In the present study, we minimized systematic semantic–grammatical confounds by using verbs and nouns referring only to events. This represents a departure from previous studies contrasting action verbs to object nouns. To examine modality-related semantic effects across grammatical classes of verbs and nouns, we used words referring to motion events and words referring to sensation events. Whereas a wealth of studies have investigated modality-related semantic effects for languages have more morphologically inflected verb than noun events. This represents a departure from previous studies contrasting action verbs to object nouns. To examine modality-related semantic effects across grammatical classes of verbs and nouns, we used words referring to motion events and words referring to sensation events. Whereas a wealth of studies have investigated modality-related semantic effects for objects (for a review, see Martin and Chao 2001), very few imaging studies have investigated modality-related semantic effects for words in other domains, such as events (James and Gauthier 2003; Hauk and others 2004; Tettamanti and others 2005). Moreover, within the event domain, to our knowledge, only 1 study has compared words belonging to different categories (motion and cognition) (Grossman and others 2003). Finally, we minimized confounds associated with explicit task demands by using an
attentive listening paradigm. Removal of any explicit decision components controlled for potential interactions between grammatical class and task demands, allowing us to investigate the possibility that functional activation might be driven by morphological differences between nouns and verbs, as argued by some authors (Shapiro and Caramazza 2003; Tyler and others 2004).

Methods

Participants
Twelve right-handed Italian native speakers (8 males, 4 females; age 37–57 years) volunteered to participate in the study. All subjects gave written informed consent, and the study was approved by the local research ethics committee.

Materials
There were 4 active conditions and 1 baseline condition. Stimuli for all active conditions were single words referring to events. The motor conditions, motor nouns (MNs) and motor verbs (MVs), used words referring to events involving motion. The sensory conditions, sensory nouns (SNs) and sensory verbs (SVs), used words referring to events involving sensory experience (see Table 1 for examples and Supplementary Data for a full list of the words used). Stimuli were selected from an initial pool of nouns and verbs following Vigliocco and others (2004). A separate group of speakers provided lists of properties that they considered salient in defining and describing a large set of words. These properties were then classified as motor, sensory (visual, acoustic, tactile, etc), functional (i.e., referring to the function served by the event), and others (i.e., mostly encyclopedic information about the events). Words with a greater proportion of motor than any other features were selected for the 2 motor conditions (average percentage of motor features: MNs = 44.17, MVs = 51.44; sensory features: MNs = 14.26, MVs = 11.53), whereas words with a greater proportion of sensory than any other features were selected for the 2 sensory conditions (average percentage of sensory features: SNs = 45.99, SVs = 47.00; motor features: SNs = 19.83, SVs = 18.89). Because only a small number of sensory words meeting the inclusion criteria was available for each sensory modality, we included words referring to several sensory modalities (vision, audition, smell, touch, and taste) in the 2 sensory conditions.

We used inflected word forms in order to increase the likelihood that morphological processes relevant to verb and noun processing were engaged. Half of the nouns were presented as singular and half as plural forms; half of the verbs were presented in the 3rd person singular and half in the 3rd person plural. Note that words in Italian are unambiguously marked as verbs and nouns, unlike in English where there is verb–noun homonymy (e.g., the fact that the English word “walk” can be used both as a noun—“the walk”—or a verb—“to walk”).

Verbs and nouns did not differ in familiarity, age of acquisition (AoA), or imageability, as established in a norming study using a group of 30 additional native Italian speakers. However, sensory words were judged as less familiar ($F_{1,311} = 20.043, P < 0.001$), acquired later ($F_{1,311} = 21.509, P < 0.001$), and less imageable ($F_{1,311} = 3.835, P < 0.001$) than motor words. Descriptive statistics are reported in Table 2. No interactions between semantic content and grammatical class were identified for any of these variables.

The baseline condition consisted of spectrally rotated versions of the word stimuli from all 4 active conditions. Rotated speech retains the acoustic complexity and some of the phonetic features of speech but is unintelligible (Blesser 1972) and therefore controls for much of the lower level perceptual processing of speech.

PET Scanning
Positron emission tomography (PET) data were obtained with a Siemens HR+/966 PET scanner operated in high-sensitivity 3-dimensional mode, using radio-labeled water ($H_2^{15}O$) as the tracer to demonstrate changes in regional cerebral blood flow (rCBF). Each subject underwent 2 scans for each of the 4 active conditions and 8 baseline scans. During each scan, a prerecorded block of stimuli from one of the experimental conditions was presented via headphones using an MP3 player, at a rate of 30 words per minute. The contents of each stimulus block were identical for all subjects, but block order was randomized for each participant. Subjects were instructed simply to listen attentively to the stimuli, with no explicit task demands or response requirements imposed. Eleven subjects also underwent structural magnetic resonance imaging (MRI) scanning (MRI was contraindicated in 1 subject) to assist in preprocessing of PET data and aid anatomical localization of functional activations.

Image preprocessing and statistical analysis were performed using SPM99 software (Wellcome Department of Cognitive Neurology, Queen Square, London; http://www.fil.ion.ucl.ac.uk). PET images (voxel dimensions $2.1 \times 2.1 \times 2.4$ mm) were realigned to remove the effects of head movement between scans and coregistered to each subject’s structural MRI. Coregistered PET and MRI images were normalized into standard Montreal Neurological Institute (MNI) stereotactic space, using parameters derived from normalization of structural MRI images to a T1-weighted MRI template. For the single subject in whom MRI was contraindicated, realigned PET images were normalized to a PET template in MNI space. Normalized PET images (2 mm isotropic voxels) were smoothed using an isotropic 12-mm full-width at half-maximum Gaussian kernel to account for individual variation in gyral anatomy and to improve the signal-to-noise ratio. Group PET data were analyzed using a random-effects model. First level analysis included scan order as a covariate controlled for potential interactions between semantic content and grammatical class.

### Table 1

Examples of word stimuli used in the 4 active experimental conditions

<table>
<thead>
<tr>
<th>Nouns</th>
<th>Verbs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Motion</td>
<td>Gravetta (shovel)</td>
</tr>
<tr>
<td></td>
<td>Tuffi (drives)</td>
</tr>
<tr>
<td></td>
<td>Atterraggio (landing)</td>
</tr>
<tr>
<td></td>
<td>Sabbata (sand)</td>
</tr>
<tr>
<td>Sensory</td>
<td>Solletico (tickles)</td>
</tr>
<tr>
<td></td>
<td>Lampe (lighting-plural)</td>
</tr>
<tr>
<td></td>
<td>Occlusa (darkness)</td>
</tr>
<tr>
<td></td>
<td>Ronzi (buzzes)</td>
</tr>
</tbody>
</table>

Note: Italian English translations are given in square brackets.

### Table 2

Mean familiarity, AoA, and imageability ratings (standard deviation in parentheses) for the words used in the different conditions

<table>
<thead>
<tr>
<th></th>
<th>Familiarity</th>
<th>AoA</th>
<th>Imageability</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sensory nouns</td>
<td>5.27 (1.17)</td>
<td>5.16 (1.66)</td>
<td>5.08 (0.84)</td>
</tr>
<tr>
<td>Sensory verbs</td>
<td>5.22 (0.53)</td>
<td>5.35 (1.53)</td>
<td>5.15 (0.57)</td>
</tr>
<tr>
<td>Motion nouns</td>
<td>5.55 (0.82)</td>
<td>4.50 (1.41)</td>
<td>5.45 (0.50)</td>
</tr>
<tr>
<td>Motion verbs</td>
<td>5.82 (0.72)</td>
<td>4.45 (1.45)</td>
<td>5.62 (0.55)</td>
</tr>
</tbody>
</table>

### Table 3

Preferential activation associated with semantic category

<table>
<thead>
<tr>
<th>Peak location</th>
<th>BA</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>Z score</th>
</tr>
</thead>
<tbody>
<tr>
<td>Motor words vs. sensory words</td>
<td></td>
<td>Left precentral gyrus</td>
<td>4</td>
<td>−40</td>
<td>−12</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Left central sulcus</td>
<td>4/3</td>
<td>−40</td>
<td>−20</td>
</tr>
<tr>
<td>Sensory words vs. motor words</td>
<td></td>
<td>Posterior left inferior frontal sulcus</td>
<td>8/9</td>
<td>−52</td>
<td>12</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Anterior left inferior temporal gyrus</td>
<td>20</td>
<td>−56</td>
<td>−12</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Anterior left inferior temporal sulcus</td>
<td>20/21</td>
<td>−60</td>
<td>−4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Left ventrolateral frontal cortex</td>
<td>10</td>
<td>−50</td>
<td>52</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Anterior left IFG</td>
<td>47</td>
<td>−48</td>
<td>36</td>
</tr>
</tbody>
</table>

Significant activation peaks for the contrasts of motor words vs sensory words and sensory words vs motor words (see Fig. 1) are listed. Anatomical locations and corresponding BA s for each activation peak were determined from the stereotactic atlas of Talairach and Tournoux (1988). Coordinates (in millimeters) refer to the location of peak voxels in MNI stereotactic space. Statistical threshold was set at $P < 0.001$, uncorrected, cluster extent threshold 50 voxels.
a nuisance variable and a blocked analysis of covariance with global counts as confound to remove the effect of global changes in perfusion across scans. At the 1st level, images of the contrast of parameter estimates were created for each subject for the following effects of interest:

1. \((MN + MV) - (SN + SV)\), to identify regions preferentially activated by motor words.
2. \((SN + SV) - (MN + MV)\), to identify regions preferentially activated by sensory words.
3. \((MV + SV) - (MN + SN)\), to identify regions preferentially activated by verbs.
4. \((MN + SN) - (MV + SV)\), to identify regions preferentially activated by nouns.

For each effect of interest, contrast images from each subject were entered into a 2nd-level analysis. One-sample \(t\)-tests were used to generate statistical parametric maps of the \(t\)-statistic at each voxel, allowing identification of voxels demonstrating significant differences in activation between motor and sensory words and between verbs and nouns. In order to maximize the chance of detecting small experimental effects while minimizing false-positive clusters, the threshold for significance for 2nd-level analyses was set at \(P < 0.001\), uncorrected, with a cluster extent threshold \((k)\) of 50 voxels. Statistical parametric maps were displayed on a mean MRI image created by averaging the structural MRIs available for 11 of the 12 subjects.

**Results**

Whole-brain analyses demonstrated that experimental manipulation of semantic category, but not grammatical class, produced significant differences in cortical activation within the left hemisphere. Preferential activation was identified for motor words relative to sensory words in left precentral gyrus motor cortical regions (Fig. 1 and Table 3). Preferential activation for sensory words was identified in 3 left hemisphere cortical regions (Fig. 1 and Table 3): anterior inferior temporal gyrus, anterior ventral prefrontal cortex including Brodmann area (BA) 47, and posterior inferior frontal sulcus. No regions of significant left hemisphere cortical activation were identified for either nouns or verbs.

As motor and sensory words differed in terms of imageability, familiarity, and AoA ratings (see Methods), we conducted further analyses to exclude the possibility that motor- and sensory-related activations were influenced by these factors. Mean imageability, familiarity, and AoA ratings were calculated for the stimulus block presented during each scan. Separate whole-brain multiple regression analyses, using mean-centered covariate vectors for the factors imageability, familiarity, and AoA, were conducted in SPM99 for motor and sensory words (with scan order included as a nuisance variable). Separate contrasts were used to generate statistical parametric maps of voxels demonstrating significant positive or negative correlations between rCBF and each of the 3 factors. For each analysis, search volumes were limited to the clusters identified previously as showing preferential responses to either motor or sensory words. In the left precentral gyrus cluster activated by motor words, no voxels demonstrated a significant correlation.

Figure 1. Preferential activation associated with semantic category. Significant activation for motor words compared with sensory words (red) and for sensory words relative to motor words (blue) is shown projected onto a rendered template brain surface in MNI stereotactic space. Detailed sagittal, axial, and coronal views of activation foci located in left primary motor cortex, anterior left IFG (BA 47), and anterior left inferior temporal gyrus are displayed on a mean MRI image created from structural MRIs available from 11 of the 12 subjects (see Methods), with crosshairs located at peak voxels (numbers indicate MNI space coordinates, in millimeters). Threshold for statistical significance is \(P < 0.001\), uncorrected, cluster extent threshold 50 voxels.
between rCBF and stimulus familiarity, imageability, or AoA (P < 0.05, small-volume corrected). Similarly, no voxels in the left prefrontal and inferior temporal clusters activated by sensory words demonstrated a significant correlation between rCBF and stimulus familiarity, imageability, or AoA (P < 0.05, small-volume corrected).

Although the most consistent evidence for distinct neural representations of grammatical class has come from the demonstration of verb-specific activation in left IFG (see Introduction), we did not find grammatical class effects in this region. To definitively exclude the possibility of weak grammatical class effects in left IFG, we supplemented the whole-brain analyses described above with region of interest (ROI) analyses of left IFG activation. ROI analyses were performed using the MarsBaR software toolbox within SPM99 (Brett and others 2002). Using an electronic atlas of BAs (Maldjian and others 2003), left IFG was divided into 3 ROIs, corresponding to BAs 47, 45, and 44, respectively. For each of these ROIs, individual measures of mean effect size for each of the 4 active conditions relative to the rotated speech baseline condition were obtained in each subject. Statistical analysis of mean activation values was conducted separately for each ROI, using a 2-way repeated-measures analysis of variance (ANOVA) with factors semantic category and grammatical class. ANOVAs demonstrated a significant main effect of semantic category in BA 45 (F1,11 = 6.616, P < 0.05) and BA 47 (F1,11 = 7.078, P < 0.05). In both these regions, activation was significantly greater for sensory words than motor words. There was no significant effect of semantic category in BA 44 (Fig. 2). There was no significant main effect of grammatical class, or semantic category × grammatical class interaction, in any of the ROIs.

**Discussion**

This study is the first to assess the independent contributions of semantics and grammatical class to the neural organization of word knowledge. It is also the 1st study to investigate semantic differences for words referring to events characterized on the basis of motor and sensory properties. In contrast to previous studies, we attempted to orthogonalize the effects of semantics and grammatical class. Verb–noun segregation was optimized by virtue of the absence of verb–noun homonymy in Italian and by the use of inflected verb and noun forms. To avoid systematic semantic differences between verbs and nouns, we used words referring only to events. Although this avoided semantic–grammatical confounds, it rendered the semantic manipulation across grammatical class less clear-cut. As events are by nature dynamic, the sensory words all possessed some motor features. Similarly the motor words possessed some sensory features (e.g., the motor words were highly imageable). Nonetheless, we were able to introduce a relative semantic difference between motor and sensory words, allowing valid comparison between these conditions.

We identified preferential activation for motor over sensory words in the left hemisphere motor cortical regions. This result suggests a correspondence between motor representations of actions and representations of the meaning of action-related words, a finding in line with previous studies showing motor and premotor activations in reading words or listening to sentences referring to actions (Hauk and others 2004; Tettamanti and others 2005). In previous studies, the human visual motion area, area MT, in temporooccipital cortex has been implicated in the processing of action words (Damasio and others 2001), even when the same words (e.g., “hammer”) are contrasted as actions and objects (Tranel and others 2005). The absence of preferential motor word activation in area MT in the present study may reflect differences in experimental task. The present study used an implicit auditory comprehension paradigm, whereas the studies of Damasio and others (2001) and Tranel and others (2005) involved picture naming; a previous
study involving word reading without an explicit generation task also failed to observe activation in area MT (Hauk and others 2004).

Sensory word processing preferentially activated regions in left anterior inferior temporal gyrus, and anterior IFG and the posterior inferior sulcus. Anterior inferior temporal cortex and adjacent fusiform gyrus cortex have been implicated in semantic processing of both pictures and words (Vandenberghhe and others 1996; Mummery and others 1998; Giraud and Price 2001; Crinion and others 2003; Sharp and others 2004a, 2004b). Lesions of these areas have been associated with specific deficits for sensory-defined concepts, as shown in the seminal work by Warrington and Shallice (1984) (for additional cases also extending beyond the visual modality, see also Borgo and Shallice 2001; Siri and others 2003). Anterior inferior temporal cortex contains high-order visual association cortex and is adjacent to several heteromodal cortical regions (middle temporal gyrus, medial fusiform gyrus, parahippocampal region) receiving input from multiple sensory modalities (Gloor 1997; Mesulam 2000). Therefore left inferior temporal activation for sensory words seen in the present study could be explained in terms of the rich multisensory properties of these words. Previous studies demonstrating inferior temporal activation with word processing involved words referring to objects; the present result, using words referring to events, suggests that words rich in sensory properties activate stored sensory representations, regardless of their content domain (objects or actions).

Taken together, the motor cortical activation for motor words and the inferior temporal cortical activation for sensory words provide evidence for the view that a distributed system of modality-specific featural representations underlies lexical semantics (Martin and Chao 2001; Tranel and others 2001; Barsalou and others 2003; Damasio and others 2004). Such a system is implicitly activated in the automatic process of spoken word comprehension. These findings are inconsistent with theories in which implicit language comprehension activates only propositional conceptual representations and not modality-related information (e.g., Jackendoff 2002). Preferential activations for motor and sensory words could not be accounted for by differences in linguistic factors such as familiarity, imageability, and AoA, as these factors did not correlate with rCBF in motor- and sensory-responsive regions.

Whole-brain and ROI analyses demonstrated that sensory words preferentially activated anterior portions of left IFG cortex, in addition to temporal areas. Specifically, sensory word processing activated BA 45 and BA 47, but not BA 44. Previous functional imaging studies have provided evidence of functional specialization within subregions of left IFG for different aspects of language comprehension, implicating posterior IFG (BA 44) in syntactic (Dapretto and Bookheimer 1999; Embick and others 2000; Newman and others 2003) and phonological (Poldrack and others 1999; Devlin and others 2003) processes and anterior IFG (BAs 45 and 47) in semantic processing (Dapretto and Bookheimer 1999; Poldrack and others 1999; Bookheimer 2002; Devlin and others 2003; Newman and others 2003). Our results also demonstrate that activation in anterior portions of left IFG is driven by semantic factors. In the present study, activation within left anterior IFG was greater for the sensory semantic category. Sensory words differed systematically from motor words in terms of lexical familiarity, imageability, and AoA. Greater anterior IFG activation for sensory words may have reflected a requirement for more effortful semantic processing of less familiar, less imageable, or later-acquired words, although no direct correlations between these linguistic factors and rCBF responses were found in this region.

Using materials that avoided a systematic verb action and noun object confound, and a paradigm that does not require selection and decision processes, we found that brain activation during implicit comprehension of verbs and nouns referring to events did not differ on the basis of grammatical class. This result is consistent with the hypothesis that the neural substrates of implicit single-word processing are determined principally by semantic rather than grammatical factors. In using verbs and nouns referring only to events, our study represents a departure from previous work that has used object-related nouns. It might therefore be argued that our result reflects a peculiarity of event-related words and is irrelevant to words covering the domain of concrete entities. However, we argue that if different neural networks subserve the processing of verbs and nouns, differential activation should occur regardless of the semantic domain the words come from. Our results are supported by data from a neuropsychological study investigating grammatical class effects on word retrieval (Collina and others 2001). In this study, aphasic stroke patients showed differences in their ability to retrieve object- and event-referent nouns, but no differences in performance for retrieval of nouns and verbs referring to events.

In contrast to previous studies (Perani and others 1999; Tyler and others 2004), we did not observe verb-specific activations in left IFG. Verb-specific activation in left IFG, in particular in BA 44, has been found in studies that involved explicit tasks. Left IFG has been shown to be involved in response selection during controlled processing of language (Gold and Buckner 2002; Binder and others 2004), and in particular in selecting a response from competing alternatives (Thompson-Schill and others 1997). In most languages, verbs tend to have more morphologically inflected forms than nouns, thus decision-based tasks (such as lexical or semantic decision) require the speaker to consider or select from a greater number of word forms for verbs than nouns. This raises the possibility that these apparently verb-specific responses were a consequence of an interaction between grammatical class and task demands, rather than reflecting true grammar-based or morphological variations in processing verbs and nouns. Demands on decision and selection processes, combined with these differences in inferential alternatives, may therefore account for differences observed during production of inflected verb and noun forms during functional imaging (Tyler and others 2004; Shapiro and others 2005) and transcranial magnetic stimulation (Shapiro and others 2001) studies. In addition, demands on decision and selection processes may vary significantly between languages: for example, Italian has up to 47 inflected verb forms, marking person, number, tense, etc. (Bates and others 2001), whereas English has a maximum of 5 inflected forms. Interaction between grammatical class and language-specific task demands may explain why activation of left IFG has been found in studies using lexical decision in Italian (Perani and others 1999) but not in English (Tyler and others 2001).

We used an implicit comprehension paradigm in order to avoid the potential confounds of task demands. Although such a paradigm does not allow monitoring of the participants' behavior during scanning, this disadvantage is outweighed by
the benefits of being able to study word processing under conditions that more closely approach natural automatic word comprehension. The use of this paradigm and inflected Italian words provided also the opportunity to test whether left IFG activation reflects decision and selection processes (as discussed above) or greater engagement of morphological processes for verbs than nouns at the single-word level (Shapiro and Caramazza 2003; Tyler and others 2004). Because there are many more inflectional forms for verbs than nouns in Italian, the fact that we did not observe preferential activation for Italian verbs in left IFG does not support the involvement of this region in automatic morphological processing.

In conclusion, in the absence of systematic verb–noun semantic differences and explicit task demands, no differential cortical activation for verbs or nouns was observed, whereas we found specific activations driven by the semantic differences between our stimuli. Verb-specific activation was not seen despite the compelling morphological differences between Italian verbs and nouns. Our findings suggest that comprehension of verbs and nouns is not mediated by distinct cortical substrates but rather takes place within a common language network where neural organization is dictated by semantic content. By no means do we argue that grammatical class is irrelevant to language processing. Recent behavioral studies in German and Italian show that grammatical class affects production latencies when speakers produce sentences but not when they produce single words (Pechmann and others 2004; Vigliocco and others 2005), and grammatical class information must be used by listeners and speakers when processing connected speech. However, our results do call into question the view that grammatical class per se drives neural segregation within the language network at the lexical level.

**Supplementary Material**

Supplementary material can be found at: http://www.cercor.oxfordjournals.org/

**Notes**

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