The role of semantics and grammatical class in the neural representation of words

Gabriella Vigliocco[1], Jane Warren[2,3], Simona Siri[4], Joanne Arcuili[1,] Sophie Scott[5], Richard Wise[2,3]

1. Department of Psychology, University College London, UK
2. Division of Neuroscience and Mental Health, Imperial College London
3. MRC Cyclotron Unit, Hammersmith Hospital, London, UK
4. Department of Psychology and Neuroscience, Vita Salute University, Milan, Italy
5. Institute of Cognitive Neuroscience, University College London, UK

Corresponding author: Gabriella Vigliocco Department of Psychology, University College London, Gower Street, WC1 6BT. Email: g.vigliocco@ucl.ac.uk. Phone: +44-20-76795345

Running Title: Neural Correlates of Meaning and Syntax

ABSTRACT

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 (PET) 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, while 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: Language; PET; Semantics; Grammatical class; 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 *et al*., 2004). More recently, imaging studies have implicated motor and premotor cortices (Hauk *et al*., 2004; Tettamanti *et al*., 2005), and middle temporal regions (Martin *et al.,* 1995; Tranel *et al*., 2005) including the visual motion area MT (Damasio *et al*., 2001; Tranel *et al*., 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 & Shallice, 1984; Martin & Chao, 2001; Damasio *et al*. 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 & Hillis, 1991; Damasio & Tranel, 1993; Daniele *et al*., 1994; Silveri & DiBetta, 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 *et al*., 1999; Tyler *et al*., 2004; Shapiro *et al.,* 2005), although this has not been a universal finding (Tyler *et al*., 2001).

However, word meaning and grammatical class are highly correlated in most languages: verbs refer to actions or other events while 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 *et al*., 1999; Tyler *et al*., 2004), so that verb-specific activation may reflect processing of action-related knowledge (Grezes & Decety, 2001) rather than grammatical class. In addition, previous studies showing verb-specific left IFG activation used explicit tasks, such as lexical (Perani *et al*., 1999) or semantic (Tyler *et al*., 2004) decision or a task in which participants had to produce inflected forms of verbs and nouns in response to a cue (Shapiro *et al*., 2005). Because most languages have more morphologically inflected verb than noun forms (e.g., in English there are at least four different forms for verbs and only two for nouns), task performance on verbs may place greater demands on selection and decision processes attributed to left IFG (Thompson-Schill, *et al*., 1997; Gold & Buckner, 2002; Binder, *et al*., 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 effects for objects (see Martin & Chao, 2001 for a review), very few imaging studies have investigated modality-related semantic effects for words in other domains, such as events (Hauk *et al.,* 2004; James & Gauthier, 2003; Tettamanti *et al*., 2005). Moreover, within the event domain, to our knowledge only one study has compared words belonging to different categories (motion and cognition) (Grossman *et al.*, 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 & Caramazza, 2003; Tyler *et al.,* 2004).

METHODS

Participants

Twelve right-handed Italian native speakers (eight male, four female; age 37-57) 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 four active conditions and one 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 *et al*. (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 encyclopaedic information about the events). Words with a greater proportion of motor than any other features were selected for the two Motor conditions (average percentage of motor features: MNs=44.17; MVs=51.44; sensory features: MNs=14.26; MVs=11.53), while words with a greater proportion of sensory than any other features were selected for the two 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 two Sensory conditions.

We used inflected wordforms 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 third person singular and half in the third 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 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 ($F(1,311) = 20.043$, $p < .001$); as acquired later ($F(1,311) = 21.509$, $p < .001$); and as less imageable ($F(1,311) = 3.835$, $p < .001$) 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 four 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

PET data was obtained with a Siemens HR++/966 PET scanner operated in high-sensitivity 3D mode, using radio-labelled water ($H_2{}^{15}O$) as the tracer to demonstrate changes in regional cerebral blood flow (rCBF). Each subject underwent two scans for each of the four active conditions, and eight baseline scans. During each scan, a pre-recorded 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 MRI scanning (MRI was contraindicated in one subject) to assist in pre-processing of PET data and aid anatomical localisation of functional activations.

Image pre-processing 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 x 2.1 x 2.4mm) 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 normalised into standard MNI (Montreal Neurological Institute) stereotactic space, using parameters derived from normalisation of structural MRI images to a T1-weighted MRI template. For the single subject in whom MRI was contraindicated, realigned PET images were normalised to a PET template in MNI space. Normalised PET images (2mm isotropic voxels) were smoothed using an isotropic 12mm full-width at half-maximum (FWHM) Gaussian kernel to account for individual variation in gyral anatomy and to improve the signal-to-noise ratio. Group PET data was analysed using a random-effects model. First level analysis included scan order as a nuisance variable, and a blocked ANCOVA (analysis of covariance) with global counts as confound to remove the effect of global changes in perfusion across scans. At the first level, images of the contrast of parameter estimates were created for each subject for the following effects of interest:

1. (MNs + MVs) – (SNs + SVs), to identify regions preferentially activated by Motor words.
2. (SNs + SVs) – (MNs + MVs), to identify regions preferentially activated by Sensory words.
3. (MVs + SVs) – (MNs + SNs), to identify regions preferentially activated by Verbs.
4. (MNs + SNs) – (MVs + SVs), to identify regions preferentially activated by Nouns.

For each effect of interest, contrast images from each subject were entered into a second-level analysis. One-sample *t*-tests were used 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 maximise the chance of detecting small experimental effects while minimising false positive clusters, the threshold for significance for second-level analyses was set at $p < 0.001$, uncorrected, with a cluster extent threshold 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 (Figure 1A, Table 2). Preferential activation for Sensory words was identified in three left hemisphere cortical regions (Figure 1B, Table 2): anterior inferior temporal gyrus, anterior ventral prefrontal cortex including 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 age of acquisition (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 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 three 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 between rCBF and stimulus familiarity, imageability or age of acquisition ($p < 0.05$, 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 age of acquisition ($p < 0.05$, 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 inferior frontal gyrus (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 analyses of left IFG activation. _Region-of-interest analyses were performed using the MarsBaR software toolbox within SPM99 (Brett *et al.*, 2002). Using an electronic atlas of Brodmann areas (Maldjian *et al.*, 2003), left IFG was divided into three regions of interest (ROIs), corresponding to Brodmann areas (BAs) 47, 45 and 44 respectively. For each of these ROIs, individual measures of mean effect size for each of the four 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 two-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 ($F(1,11) = 6.616$, $p < 0.05$) and in BA 47 (F (1,11)

= 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. There was no significant main effect of Grammatical Class, or Semantic Category X 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 first 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 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 *et al.*, 2004; Tettamanti *et al.*, 2005). In previous studies, the human visual motion area, area MT, in temporo-occipital cortex has been implicated in the processing of action words (Damasio *et al.*, 2001), even when the same words (e.g., *hammer*) are contrasted as actions and objects (Tranel *et al..,* 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, while the studies of Damasio and colleagues (Damasio *et al.*, 2001), and Tranel and colleagues (Tranel *et al.*, 2005), involved picture naming: a previous study involving word reading without an explicit generation task also failed to observe activation in area MT (Hauk *et al.*, 2004).

Sensory word processing preferentially activated regions in left anterior inferior temporal gyrus, and anterior inferior frontal gyrus 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 (Vandenberghe *et al.*, 1996; Mummery *et al.*, 1998; Giraud & Price, 2001; Crinion *et al.*, 2003; Sharp *et al.*, 2004a; Sharp *et al.*, 2004b). Lesions of these areas have been associated with specific deficits for sensory–defined concepts, as shown in the seminal work by Warrington & Shallice (Warrington & Shallice, 1984; see also Borgo & Shallice, 2001; Siri *et al.*, 2003 for additional cases also extending beyond the visual modality). Anterior inferior temporal cortex contains high-order visual association cortex, and is adjacent to several heteromodal cortical regions (superior temporal sulcus and middle temporal gyrus laterally, and paralimbic cortex medially) 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 multi-sensory 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 & Chao, 2001; Tranel *et al*., 2001; Barsalou *et al.,* 2003; Damasio *et al*.., 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 age of acquisition, as these factors did not correlate with rCBF in Motor- and Sensory-responsive regions.

Whole-brain and region-of-interest analyses demonstrated that Sensory words preferentially activated anterior portions of left inferior frontal gyrus cortex, in addition to temporal areas. Specifically, Sensory word processing activated BA45 and 47, but not BA44. 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 & Bookheimer, 1999; Embick *et al*., 2000; Newman et al., 2003) and phonological (Poldrack *et al*., 1999; Devlin *et al*., 2003) processes, and anterior IFG (BAs 45 and 47) in semantic processing (Dapretto & Bookheimer, 1999; Poldrack *et al*., 1999; Bookheimer, 2002; Devlin *et al*., 2003; Newman et al., 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 age of acquisition. 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 *et al*., 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 *et al*., 1999; Tyler *et al*., 2004), we did not observe verb-specific activations in left IFG. Verb-specific activation in left IFG, in particular in BA44, 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 (Binder *et al*., 2004; Gold & Buckner, 2002), and in particular in selecting a response from competing alternatives (Thompson-Schill *et al*., 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 wordforms 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 inflectional alternatives, may therefore account for differences observed during production of inflected verb and noun forms during functional imaging (Tyler *et al*., 2004; Shapiro *et al*.., 2005) and TMS (Shaprio et al., 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 *et al*., 2003), whereas English has a maximum of five 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 *et al*., 1999) but not in English (Tyler *et al*., 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' behaviour 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 of 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 & Caramazza, 2003; Tyler *et al*., 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 *et al*., 2004; Vigliocco *et al*., 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.

Acknowledgements: The work reported here was supported by a Biotechnology and Biological Science Research Council grant (BBSRC 31/S18749) and a Human Frontier Science Program grant (HFSP 148/2000) to Gabriella Vigliocco. Jane Warren is supported by an Action Medical Research Training Fellowship and the Barnwood House Trust (UK). Financial support for scanning costs was provided by the Medical Research Council (UK).

REFERENCES

Barsalou LW, Simmons WK, Barley AK, Wilson CD (2003) Grounding conceptual knowledge in modality-specific systems. Trends Cogn Sci 7:84-91.

Bates E , Devescovi A, Wulfeck B (2001) Psycholinguistics: A cross-language perspective. Annu Rev Psychol 52:369-396.

Binder JR, Liebenthal E, Possing ET, Medler DA, Ward BD (2004) Neural correlates of sensory and decision processes in auditory object identification. Nat Neurosci 7:295-301.

Blesser B (1972) Speech perception under conditions of spectral transformation. I. Phonetic characteristics. J Speech Hear Res 15:5-41.

Bookheimer S (2002) Functional MRI of language: New approaches to understanding the cortical organization of semantic processing. Annu Rev Neurosci 25:151-188.

Borgo F, Shallice T (2001) When living things and other 'sensory quality' categories behave in the same fashion: a novel category specificity effect. Neurocase 7:201-220.

Brett M, Anton JL, Valabregue R, Poline JB (2002) Region of interest analysis using an SPM toolbox [abstract]. Presented at the 8th International Conference on Functional Mapping of the Human Brain, June 2-6, 2002, Sendai, Japan. Available on CD-ROM in Neuroimage, Vol 16, No 2, abstract 497.

Crinion JT, Lambon-Ralph MA, Warburton EA, Howard D, Wise RJ (2003) Temporal lobe regions engaged during normal speech comprehension. Brain 126:193-201.

Caramazza A, Hillis AE (1991) Lexical organization of nouns and verbs in the brain. Nature 349:788-790.

Collina S, Marangolo P, Tabossi P (2001) The role of argument structure in the production of nouns and verbs. Neuropsychologia, 39:1125-1137.

Damasio AR, Tranel D (1993) Nouns and verbs are retrieved with differently distributed neural systems. Proc Natl Acad Sci,USA 90:4957-4960.

Damasio H, Grabowski TJ, Tranel D, Ponto LLB, Hichwa RD, Damasio AR (2001) Neural correlates of naming actions and of naming spatial relations. Neuroimage 13:1053-1064.

Damasio H, Tranel D, Grabowski TJ, Adolphs R, Damasio AR (2004) Neural systems behind word and concept retrieval. Cognition 92:179-229.

Daniele A, Giustolisi L, Silveri MC, Colosimo C, Gainotti G (1994) Evidence for a possible neuroanatomical basis for lexical processing of nouns and verbs. Neuropsychologia 32:1325-1341.

Dapretto M, Bookhiemer SY (1999) Form and content: dissociating syntax and semantics in sentence comprehension. Neuron 24:427-432.

Devlin JT, Matthews PM, Rushworth MF (2003) Semantic processing in the left inferior prefrontal cortex: a combined functional magnetic resonance imaging and transcranial magnetic stimulation study. J Cogn Neurosci 15:71-84.

Embick D, Marantz A, Miyashita Y, O'Neil W, Sakai KL (2000) A syntactic specialization for Broca's area. Proc Natl Acad Sci USA 97:6150-6154.

Giraud AL, Price CJ (2001) The constraints functional neuroimaging places on classical models of auditory word processing. J Cogn Neurosci 13:754-765.

Gloor P (1997) The temporal lobe and limbic system. New York: Oxford University Press.

Gold BT, Buckner RL (2002) Common prefrontal regions coactivate with dissociable posterior regions during controlled semantic and phonological tasks. Neuron 35:803-812.

Grezes J, Decety J (2001) Functional anatomy of execution, mental simulation, observation and verb generation of actions: a meta-analysis. Hum Brain Mapp 12:1-19.

Grossman M, Koenig P, DeVita C, Glosser G, Moore P, Gee J, Detre J, Alsop D (2003) Neural basis for verb processing in Alzheimer's disease: An fMRI study. Neuropsychology 17: 658-674.

Hauk O, Johnsrude I, Pulvermuller F (2004) Somatotopic representation of action words in human motor and premotor cortex. Neuron 22:301-307.

Jackendoff R (2002) Foundations of language: brain, meaning, grammar, evolution. Oxford: Oxford University Press.

James TW, Gauthier I (2003). Auditory and action semantic features activate sensory-specific perceptual brain regions. Curr Biol 13:1792-1796.

Levy DA, Bayley PJ, Squire LR (2004) The anatomy of semantic knowledge: Medial vs. lateral temporal lobe. Proc Natl Acad Sci USA 101:6710-6715.

Maldjian JA, Laurienti PJ, Kraft RA, Burdette JH (2003) An automated method for neuroanatomic and cytoarchitectonic atlas-based interrogation of fMRI data sets. Neuroimage 19:1233-1239.

Martin A, Haxby JV, Lalonde FM, Wiggs CL, Ungerleider LG (1995) Discrete cortical regions associated with knowledge of color and knowledge of action. Science 270:102-105.

Martin A, Chao LL (2001) Semantic memory and the brain: Structure and processes. Curr Opin Neurobiol 11:194-201.

Mesulam MM (2000) Principles of Behavioral and Cognitive Neurology (2nd edn). Oxford: Oxford University Press.

Mummery CJ, Patterson K, Hodges JR, Price CJ (1998) Functional neuroanatomy of the semantic system: divisible by what? J Cogn Neurosci 10:766-777.

Newman SD, Just MA, Keller TA, Roth J, Carpenter PA (2003) Differential effects of syntactic and semantic processing on the subregions of Broca's area. Brain Res Cog Brain Res 16:297-307.

Pechmann T, Garrett M, Zerbst D (2004) The time course of recovery for grammatical category information during lexical processing for syntactic construction. J Exp Psychol Learn Mem Cogn 30:723-728.

Perani D, Cappa SF, Schnur T, Tettamanti, M, Collina S, Rosa MM, Fazio F (1999) The neural correlates of verb and noun processing: A PET study. Brain 122:2337-2344.

Poldrack RA, Wagner AD, Prull MW, Desmond JE, Glover GH, Gabrieli JD (1999) Functional specialization for semantic and phonological processing in the left inferior prefrontal cortex. Neuroimage 10:15-35.

Price CJ (1998) The functional anatomy of word comprehension and production. Trends Cogn Sci 2:281-288.

Shapiro KA, Pascual-Leone A, Mottaghy FM, Gangitano M, Caramazza A (2001) Grammatical distinctions in the left frontal cortex. J Cognitive Neurosci 13:713-720.

Shapiro KA, Caramazza A (2003) The representation of grammatical categories in the brain. Trends Cogn Sci 7:201-205.

Shapiro KA, Mottaghy FM, Schiller NO, Poeppel TD, Fluss MO, Muller HW, Caramazza A, Krause BJ (2005) Dissociating neural correlates for nouns and verbs. Neuroimage 24:1058-1067.

Sharp DJ, Scott SK, Wise RJS. (2004a) Monitoring and the controlled processing of meaning: distinct prefrontal systems. Cereb Cortex 14:1-10.

Sharp DJ, Scott SK, Wise RJS. (2004b) Retrieving meaning after temporal lobe infarction: the role of the basal language area. Ann Neurol 56:836-846.

Silveri MC, Di Betta AM (1997) Noun-verb dissociations in brain-damaged patients: Further evidence. Neurocase 3:477-488.

Siri S, Kensinger EA, Cappa SF, Hood KL, Corkin S (2003) Questioning the living/nonliving dichotomy: evidence from a patient with an unusual semantic dissociation. Neuropsychology 17:630-645.

Talairach P, Tournoux J (1988) A stereotactic coplanar atlas of the human brain. Stuttgart: Thieme.

Tettamanti M, Buccino G, Saccuman MC, Gallese V, Danna M, Scifo P, Fazio F, Rizzolatti G, Cappa SF, Perani D (2005) Listening to action-related sentences activates fronto-parietal motor circuits. J Cogn Neurosci, 17:273-281.

Thompson-Schill, SL, D'Esposito M, Aguirre GK, Farah MJ (1997) Role of left inferior prefrontal cortex in retrieval of semantic knowledge: a reevaluation. Proc Natl Acad Sci USA 23:14792-14797.

Tranel D, Adolphs R, Damasio H, Damasio AR (2001) A neural basis for the retrieval of words for actions. Cogn Neuropsychol 18:655-670.

Tranel D, Martin C, Damasio H, Grabowski TJ, Hichwa R (2005) Effects of noun-verb homonymy on the neural correlates of naming concrete entities and actions. Brain Lang 92:288-299.

Tyler LK, Russell R, Fadili J, Moss HE (2001) The neural representation of nouns and verbs: PET studies. Brain 124:1619-1634.

Tyler LK, Bright P, Fletcher P, Stamatakis EA (2004) Neural processing of nouns and verbs: the role of inflectional morphology. Neuropsychologia 42:512-523.

Vandenberghe R, Price C, Wise R, Josephs O, Frackowiack RSJ (1996) Functional anatomy of a common semantic system for words and pictures. Nature 383:254-256.

Vigliocco G, Vinson DP, Lewis W, Garrett MF (2004) Representing the meanings of object and action words: the featural and unitary semantic space hypothesis. Cognit Psychol 48:422-488.

Vigliocco G, Vinson DP, Siri, S (2005) Semantic and grammatical class effects in naming actions. Cognition 94:B91-100.

Warrington E, Shallice T (1984) Category specific semantic impairments. Brain 107:829-854.

Table 1.

Examples of word stimuli used in the four active experimental conditions. Italian-English translations are given in square brackets.

	Nouns	**Verbs**
Motion	Giravolta *[twirl]* Tuffi *[dives]* Atterraggio *[landing]* Sobbalzi *[jerk]*	Scuote *[(s/he/it) shakes]* Galoppano *[(they) gallop]* Rincorre *[(s/he/it) chases]* Pattinano *[(they) skate]*
Sensory	Solletico *[tickle]* Lampi *[lightning-plural*] Oscurità *[darkness]* Ronzii *[buzzes]*	Annusa *[(s/he/it) sniffs]* Luccicano *[(they) shine]* Starnazza *[(it) quacks]* Degustano *[(they) taste]*

Table 2.

Mean familiarity, age of acquisition and imageability ratings (with standard deviation in brackets) for the words stimuli used in each of the experimental conditions.

	Familiarity	**Age of Acquisition**	**Imagability**
Sensory Nouns	5.27 (1.17)	5.16 (1.66)	5.08 (0.84)
Sensory Verbs	5.22 (0.93)	5.35 (1.53)	5.15 (0.57)
Motion Nouns	5.55 (0.82)	4.50 (1.41)	5.45 (0.50)
Motion Verbs	5.82 (0.72)	4.45 (1.45)	5.62 (0.55)

Table 3.

Differential activation associated with Semantic Category. Significant activation peaks for the contrasts of Motor words > Sensory words and Sensory words > Motor words (see Fig. 1) are listed. Coordinates (in mm) refer to the location of peak voxels in MNI stereotactic space. Anatomical locations and corresponding Brodmann areas for each activation peak were determined from the stereotactic atlas of Talairach & Tournoux (Talairach & Tournoux, 1988), after transformation of MNI coordinates into Talairach space. Statistical threshold was set at $p < 0.001$, uncorrected (cluster extent threshold 50 voxels).

Peak location	***Brodmann area***	***x***	***y***	***z***	***Z score***
Motor Words > Sensory Words					
Left precentral gyrus	BA 4	-40	-12	38	3.82
Left central sulcus	BA 4/3	-40	-20	44	3.45
Sensory Words > Motor Words					
Posterior left inferior frontal sulcus	BA 8/9	-52	12	36	4.44
Anterior left inferior temporal gyrus	BA 20	-56	-12	-32	4.11
Anterior left inferior temporal sulcus	BA 20/21	-60	-4	-28	3.50
Left ventrolateral frontopolar cortex	BA10	-50	52	-2	3.87
Anterior left inferior frontal gyrus	BA 47	-48	36	-6	3.56

Legends to Figures

Figure 1. Differential activation associated with Semantic Category. Significant activation for Motor words compared to 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 inferior frontal gyrus (BA 47) and anterior left inferior temporal gyrus are displayed on a mean MRI image created from stuctural MRIs available from 11 of the 12 subjects (see Methods), with crosshairs located at peak voxels (numbers indicate MNI space coordinates, in mm). The threshold for statistical significance is set at $p<0.001$, uncorrected (cluster extent threshold 50 voxels).

Figure 2. Region-of-interest analysis results. ROI analysis results are shown for each of the left BA 44, BA 45, and BA 47 regions of interest. Histogram bars represent mean effect size for the contrasts of Motor Nouns, Motor Verbs, Sensory Nouns and Sensory Verbs versus the auditory baseline condition, across all voxels within a region (error bars show standard error of the mean). Significance levels indicate results from two-way repeated-measures ANOVAs conducted separately for each ROI. Significant main effects of Semantic Category ($p<0.05$) were demonstrated for the left BA 45 and BA 47 ROIs.

Figure 1.

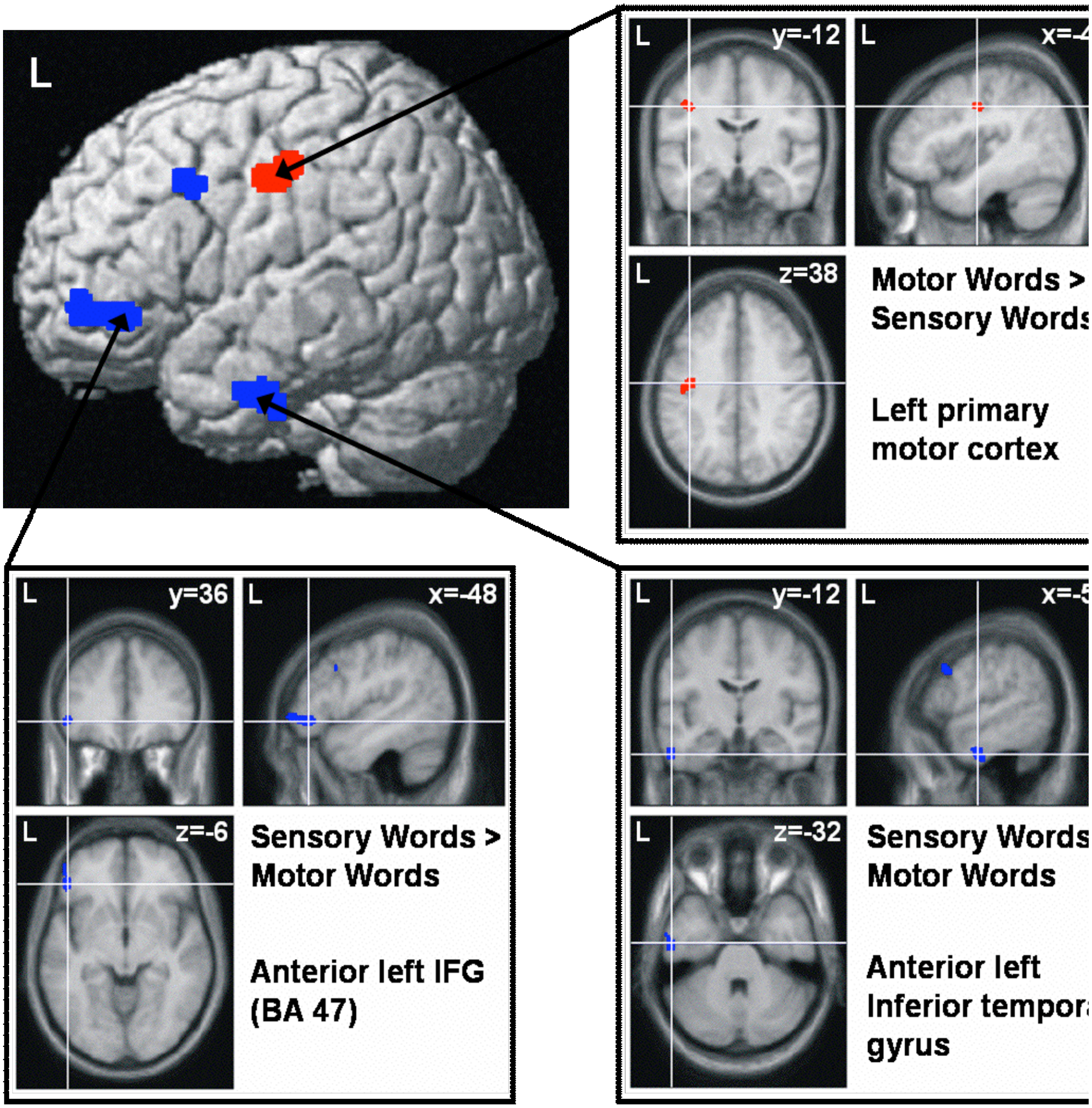
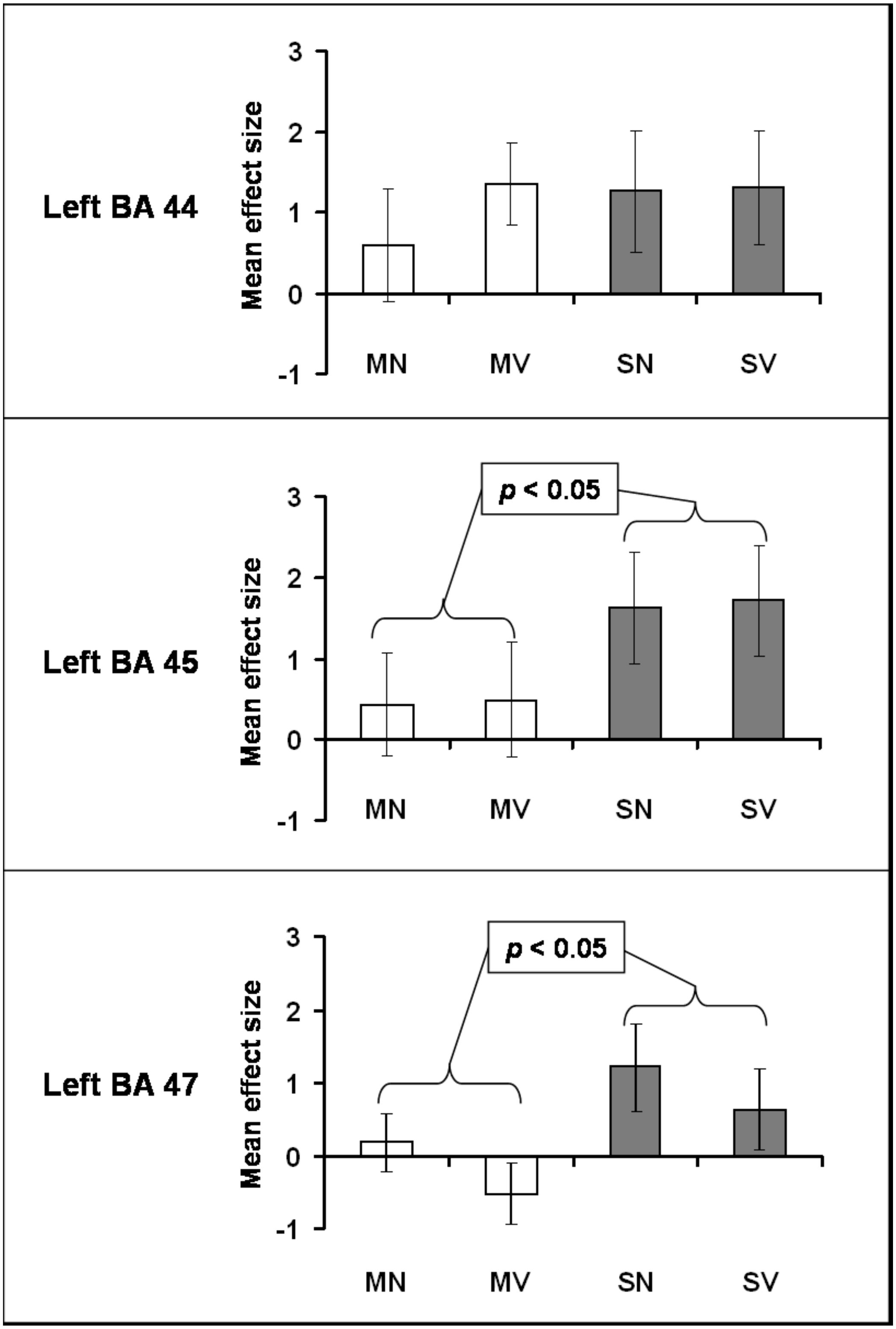

L
y=-12
L
z=38
Motor Words >
Sensory Words
Left primary
motor cortex
L
y=36
L
x=-48
L
z=-6
Sensory Words >
Motor Words
Anterior left IFG
(BA 47)
L
y=-12
L
z=-32
Sensory Words
Motor Words
Anterior left
gyrus

Figure 2.


Left BA 44
Mean effect size
3
2
1
0
-1
MN
MV
SN
SV
Left BA 45
Mean effect size
p < 0.05
3
2
1
0
-1
MN
MV
SN
SV
Left BA 47
Mean effect size
p < 0.05
3
2
1
0
-1
MN
MV
SN
SV