The neural substrate of naming events:

Effects of processing demands but not of grammatical class

Simona Siri[1], Marco Tettamanti[1], Stefano F. Cappa[1], Pasquale Della Rosa[1], Cristina Saccuman[1], Paola Scifo[1], Gabriella Vigliocco[2]

[1]Department of Psychology and Neuroscience, Vita-Salute San Raffaele University, Milano, Italy and San Raffaele Scientific Institute, Milano, Italy

[2]Department of Psychology, University College of London, London, UK

Corresponding author:
Gabriella Vigliocco
Department of Psychology
University College London
Gower Street
London WC1
Email: g.vigliocco@ucl.ac.uk
Phone: +44 20 76798687

ABSTRACT

Grammatical class is a fundamental property of language, and all natural languages distinguish between nouns and verbs. Brain activation studies have provided conflicting evidence concerning the neural substrates of noun and verb processing. A major limitation of many previous imaging studies is that they did not disentangle the impact of grammatical class from the differences in semantic correlates. In order to tease apart the role of semantic and grammatical factors, we performed an fMRI study presenting Italian speakers with pictures of events, and asked them to name them as: (1) Infinitive Verb (e.g., *mangiare* [to eat]; (2) Inflected Verb (e.g., *mangia* [(s/he) eats]); and (3) Action Noun (e.g., *mangiata* [the eating]). We did not find any verb-specific activation. However, reliable left IFG activations were found when contrasting the Action Noun with the Infinitive Verb condition. A second level analysis indicated then that activation in left IFG was greatest for Action Nouns, intermediate for Inflected Verbs and least for Infinitive Verbs. We conclude that, when all other factors are controlled, nouns and verbs are processed by a common neural system. In the present case, differences in left IFG activation emerge as a consequence of increasing linguistic and/or general processing demands.

INTRODUCTION

The neural substrate of naming events has received substantially less attention than the neural network recruited in naming objects. However, the investigation of the neural network engaged in naming events is of interest not only because it can reveal differences between these domains of knowledge, but also because it bears the potential to answer questions concerning the representation of grammatical class information.

It is well know that grammatical class plays a crucial role in language processing. For example, during language production grammatical class affects all types of errors made by normal speakers (Garrett, 1984). ERP experiments during language comprehension tasks showed that grammatical class violations in sentences produce specific responses as shortly as 200ms after presentation (Friederici, *et al.*, 1996). In a study with nouns, verbs, and class-ambiguous words, verbs elicited a left-lateralized, frontal positivity between 200 and 400 ms after stimulus onset, when used in predictable verb-context (Federmeier, *et al.*, 2000). ERP differences between verbs and nouns were also found between 300 and 800 ms after stimulus onset during a semantic priming task (Khader *et al.*, 2003).

There is also evidence that grammatical class affects the performance of language-disorders patients. A double dissociation between noun and verb processing is well documented in the neuropsychological literature, with some patients showing a disproportionate deficit with verbs compared to nouns (Rapp and Caramazza, 1997; Daniele et al., 1994; Miceli et al.,1984; Miozzo et al., 1994), and others showing the reverse pattern (Damasio & Tranel, 1993; Zingeser & Berndt, 1990; Silveri et al., 2003). This double dissociation has been linked to lesions involving different anatomical sites. Patients with verb specific impairments often have anterior lesions, usually involving the left prefrontal cortex (e.g., Daniele, 1994), whereas patients with noun specific impairments generally show left temporal lesions (Damasio, 1993). Moreover, it has been reported that patients with fronto-temporal dementia showed a greater action naming impairment compared to patients suffering from Alzheimer disease (Cappa et al., 1998).

Neuroimaging studies in normal subjects, however, have provided only limited support to these lesion-based hypotheses proposing a neural separation between noun and verb processing. The discrepancies among the studies may be attributed to a number of factors. Most important, the vast majority of previous patient and imaging studies investigating differences in noun and verb processing did not distinguish between grammatical class and the semantic correlates of grammatical class. Across languages, the distinction between nouns and verbs is rooted in the distinction between objects and actions (see Vigliocco *et al*. 2004; Vinson & Vigliocco, 2002 for a discussion). Most previous studies used as stimuli nouns referring to objects and verbs referring to actions, introducing therefore a confound between grammatical and semantic class. In the imaging literature, this is the case in early studies using verb-generation (Martin *et al*., 1995; Petersen *et al*., 1988, 1989; Warburton *et al*., 1996), but also in more recent studies using picture naming (Tranel et al., 2005).

Studies that attempted to lessen the semantic confound by using both concrete and abstract nouns and verbs provided mixed results. In a lexical decision study by Perani *et al* in Italian (1999) using concrete and abstract nouns and verbs, verb-specific activations were reported in left IFG but no noun-specific activations were observed. This finding was replicated in English in a semantic decision study using inflected nouns and verbs (Tyler *et al*., 2004), but not in a lexical decision study using uninflected words (Tyler *et al*., 2001). Greater left IFG activations for verbs than nouns in these previous studies might have not reflected grammatical class differences, but morphosyntactic processes that may be more demanding for verbs than nouns, if not simply greater processing demands imposed by verbs than nouns (see Binder *et al*, 2004; Thompson-Schill *et al*., 1997; Vigliocco *et al*., 2006). These findings arise because 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. It should also be noted that 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), so 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), in a way that verb-specific activation may result from an interaction between grammatical class and task demands. This possibility has been tackled in a study by Longe *et al*. (2006). Greater activations of left IFG for verbs than nouns were observed when English speakers made semantic judgements on inflected words but not when they made judgements on the same words presented in an uninflected form. However, as discussed in Shapiro *et al*. (2006), it can be argued that this specific task does not engage grammatical class information for uninflected words.

In an attempt to control for the semantic correlates of noun-verb differences,, in a fMRI study, Shapiro and colleagues (2006) considered only areas of significant activations emerging both when speakers were producing phrases in response to real words (either object-nouns, action-verbs but also more abstract nouns and verbs) and when speakers were producing phrases in response to pseudowords. Moreover, in order to control for morphophonological correlates of grammatical class differences, only areas of significant activation when speakers were producing both regularly and irregularly inflected nouns and verbs were considered. Across three experiments, participants were presented with words (either a noun or a verb) or pseudowords (to be used in either a noun or verb context) and their task was to produce short phrases such as *many doors*, or *he sweeps*. Significant greater activations for nouns across experiments were observed within the left fusiform gyrus (BA 20). Significant greater activations for verbs were found in left prefrontal cortex (BA 9) and in left superior parietal cortex (BA 7). However, it can be argued that the stimuli used in this study still conflate semantics and grammatical class. It has been proposed, in fact, that the mental representation for nouns and verbs develops around an initial distinction between prototypical nouns, that are objects and prototypical verbs, that are actions (Bates *et al,* 1982; O'Grady, 1997; Gauthier *et al.*, 1999). In this view, when presented with novel words, speakers infer prototypical semantic properties of objects, if these words are used in "noun" contexts, and prototypical semantic properties of actions, if they are used in "verb" contexts. The finding of fusiform activations just anterior to the areas involved in object recognition for nouns, and the frontoparietal activations for verbs in the Shapiro *et al.* (2006) may thus still reflect semantic differences between nouns and verbs.

A different approach to controlling for the semantic correlates of grammatical class was used in a PET study by Vigliocco *et al.* (2006) in Italian. In this study, only words referring to events, either nouns (e.g., *corsa* [run]) or verbs (e.g., *galoppa* [(s/he) gallops]), and either referring to sensation (e.g., *solletico* [tickle]) or motion (e.g., *giravolta* [twirl]) were used. Participants were presented auditorily with blocks of sensory or motor nouns or verbs and asked to simply listen to the words. Whereas significant activations related to differences between sensory and motion words were found in anterior temporal cortex, for sensory words and in primary motor cortex, for motion words, no specific activations for nouns or verbs were observed. However, again, one may argue that just listening to single words (even if inflected) may not engage grammatical class information.

The fMRI experiment we report here provides a further test of grammatical class differences when semantics is controlled in an attempt to better understand the conflicting results reported in the literature. Using a mini-block design, we asked native Italian speakers to name the <u>same</u> picture of an event as follows.

(1) Infinitive Verb (e.g., *mangiare* [to eat]

(2) Inflected Verb (e.g., *mangia* [(s/he) eats])

(3) Action Noun (e.g., *mangiata* [the eating])

Using the same picture in the different naming conditions we eliminate the semantic confound because participants name the same event using either a noun or a verb. Moreover, as the same picture is always presented, any difference cannot be attributed to visual processing demands. Using a picture naming task, we fully engage the language production system from conceptual retrieval to word retrieval, thus, if there are any differences in processing nouns and verbs these should emerge, taking in account that noun-verb dissociations in the neuropsychological literature have been established using picture naming.

A further remark is that producing the infinitive form of a verb (example 1) engages lexical retrieval processes, whereas producing the inflected form (example 2) further engages syntactic and morphophonological processes. This is because Italian is a *pro-drop* language in which the subject of a sentence does not need to be produced (as it is the case, instead, in English). Thus, an inflected verb is either a full sentence (for intransitive verbs, e.g., *cammina* [s/he walks]) or a sentence fragment (for transitive verbs, e.g., *mangia* [s/he eats]). Therefore, if activations in left IFG previously reported during verb processing are due to engagement of morpho-syntactic processes, these activations should be greater in the Inflected Verb than in the Infinitive Verb condition. Importantly, by explicitly instructing participants to name the picture using a noun or a verb, we further ensure that grammatical class information is relevant to the task (in contrast to previous studies that used words as stimuli and tasks, such as lexical decision, in which grammatical class is neither implicitly engaged nor relevant to the task, e.g., Perani *et al.,* 1999; Tyler *et al.*, 2001). Finally, as an element of novelty, we examine nouns that are morphologically complex as they are morphologically derived from verbs (example 3).

If noun and verb specific activations in previous studies emerged as a consequence of semantic differences between stimuli, we should not find any specific activation in the contrast between Infinitive Verb and Action Noun (examples 1 and 3). If previously observed verb-specific activations in left IFG were due to greater processing demands of the stimuli rather than by verb processing *per se*, we may observe left IFG activations for Action Nouns (example 3). This is because these stimuli are not only more linguistically complex (the nouns are morphologically derived from the verb), but moreover, in order to produce the noun response, speakers have to suppress the more natural verb response to the materials (i.e., given a picture of an action, if no specific naming instructions are given, speakers name it using a verb rather than the corresponding noun).

METHODS

Subjects

Twelve Italian native speakers (7 male, 5 female; mean age 26), recruited within the student population of Vita-Salute University participated in the study. All participants had no history of neurological or psychiatric disorders and were right-handed. Right-handedness was verified using the Edimburgh Inventory (Oldfield, 1971). Prior to the experiment all participants gave written consent to participate.

Materials

Seventy-two black and white line drawing depicting actions were used. These pictures were taken from the Druks and Materson's (2000) object and action naming battery. Fifty-two other pictures from this set were excluded because (a) the actions depicted could not be named as action nouns in Italian (e.g. *crawling*). (b) Name agreement in Italian, as established in a norming phase, was lower than 70%.

Experimental design

Subjects viewed black and white pictures one at a time and they were asked to name them overtly. Written instructions appearing before picture presentation indicated whether they had to produce: 1) Infinitive Verb (e.g *correre* [to run]); 2) Inflected Verb (e.g. *corre* [he/she runs]); 3) Action Noun (e.g. *corsa* [the run]) (see Figure 1 for examples of pictures and naming responses). Each picture was presented three times, once in each of the experimental runs. Each picture was available on the screen for 2.5 seconds. Instructions remained on the screen for 1.5 seconds. Type of response was changed every four, five items, introducing a mini-block design. Each picture was presented three times, one time per run, in a different condition in each run (ex. RUN1 – Infinitive Verb, RUN2 – Action Noun, RUN3 – Inflected Verb). Order of pictures within each mini-block wasrandomized and the order of experimental runs was randomized across subjects.. A mini-block design was chosen instead of a completely event-related paradigm on the basis of the results of behavioural testing that we carried out first. Fourteen subjects were tested outside the scanner using the same materials and timing. In this behavioural study we established that a mini-block design was preferable to a fully random design because this latter produced high levels of variability in the RTs, likely because of the increased difficulty of the task that continuously required subjects to switch response type. The mini-block design was combined with jittered Inter Stimulus Interval (ISI= 1, 2, or 3 s) in order to optimize statistical power (Dale, 1999).

Procedures

Pictures were presented to participants via a portable computer placed outside the magnet room equipped with Presentation 0.91 (Neurobehavioral Systems, Albany, CA, USA). A projector connected to the laptop delivered stimuli on a translucent screen placed at the foot of the magnet bore. Participants viewed the screen through a mirror system attached to the top of the head coil. Before entering in the scanner, all participants underwent a training session on a different set of pictures in order to familiarize them with the task and to optimize their performance during the experimental session. Moreover participants were trained to minimize jaw and tongue movements while naming to reduce movement artefacts. During the scanning participants were asked to speak into a plastic tube attached to the head coil and they were required to avoid head movements as much as they could. The plastic tube conveyed the sound outside the scanner room where there was a small microphone connected to a computer (for recording response times) and a tape recorder (for recording naming responses in order to score accuracy).

Imaging data acquisition and analysis

Brain imaging was conducted on a 1.5 Tesla Sigma scanner (General Electric, Milwaukee, WI, USA) equipped with a standard head coil. Twenty contiguous, gradient-echo echoplanar images, sensitive to BOLD contrast, parallel to the AC-PC were acquired using a T2* weighted gradient-echo EPI sequence (TR 2,5 s, TE 60ms, FOV 280x280, 64x64 matrix, flip angle 90°, slice thickness 4 mm, 4.375x4.375mm in-plane resolution). High-resolution T1-weighted images were also acquired (3D-SPGR sequence, TR 4.50 s, TE 9 ms, FOV 24x24 cm, matrix 256^2, slice thickness 1.5 mm).

Data processing and statistical analysis was performed with SPM2 (www.fil.ion.ucl.ac.uk). The entire volume set for each subjects was corrected for slice acquisition order and realigned to the first volume of the first sequence. Functional images were then spatially normalized to the Montreal Neurological Institute standard space to allow for group analysis. Prior to statistical analysis, all images were smoothed using an isotropic Gaussian kernel (FWHM=8mm).

The data for each subject were modelled using the general linear model (Friston et al., 1995). Three sessions and three variables were entered into the model (Infinitive Verb, Inflected Verb, Action Noun). The BOLD response for each event was modeled with the canonical haemodinamic response function (HRF) along with the time derivative. The first ten volumes of each run were discarded to allow attainance of a T2 equilibrium. Movement parameter estimates produced by the realignment procedure were entered as confound regressors in the first-level single-subject design matrices, in order to correct for potential movement artifacts caused by the overt naming task. Contrast images for the three individual conditions of all subjects were combined into a second level random effects group analysis (Basic models, One-way ANOVA) (Penny and Holmes, 2003). Within the One-way ANOVA design, we computed Student t-tests, including 1) Main effect (Infinitive Verb + Inflected Verb + Action Noun); 2) Direct comparisons (Action Noun - Infinitive Verb; Action Noun - Inflected Verb; Inflected Verb - Infinitive Verb).

We assessed the cytoarchitectonic probability of activations in the left IFLC, using the probability maps (Amunts *et al.*, 1999) for BA 44 and BA 45 available with the SPM Anatomy toolbox (http://www.fz-juelich.de/ime/spm_anatomy_toolbox).

RESULTS

Behavioral data

Response times and error rates were recorded for a group of 14 participants (Group 1, from the same population as the participants to the fMRI study) outside the scanner and for the 12 participants (Group 2) who performed the naming task during functional scanning. Data collected outside the scanner are closely comparable to data collected during fMRI and are reported here to point out that scanning did not interfere with participants' performance on the naming task and that our apparatus for recording RTs during scanning produced reliable and comparable data (see Figure 2). For both groups, statistical analyses on RTs showed that subjects were significantly slower in the Action Noun condition (Group 1: mean = 1633 ms, SD = 601; Group 2: mean = 1745 ms; SD = 563) compared to both other conditions (Tukey-Kramer HSD test $P<0.001$, for both groups), while there was no significant difference between Infinitive Verb (Group 1: mean = 1212 ms, SD = 458 ; Group 2: mean = 1409 ms; SD = 364) and Inflected Verb (Group 1: mean = 1395 ms, SD = 533; Group 2: mean = 1387 ms; SD = 389) (See Figure 2). No significant difference in accuracy was found across the three conditions and across both groups outside and inside the scanner. (Group 1: Action Nouns: 88%; Infinitive Verbs: 97%; Inflected Verbs: 96%) Group 2: Action Nouns: 88%; Infinitive Verbs: 97%; Inflected Verbs: 96%).

Functional data

First, we performed a main effect analysis including all three naming conditions ($p<0.001$, Family Wise Error (FWE) type correction). We found activations in the left inferior frontal gyrus, the left superior temporal gyrus, the temporal poles bilaterally, and the right hippocampus (Table 1, Figure 3).

Second, we performed the direct comparisons between the three naming conditions. We found significant effects ($p<0.05$, False Discovery Rate (FDR) type correction) only when we performed the subtraction Action Noun minus Infinitive Verb; these effects were exclusively located in the left IFG, both ventrally and dorso-caudally (pars opercularis, 60% probability for Brodmann Area 44, according to cytoarchitectonic probability maps (Amunts et al., 1999, Figure 4). The subtraction Action Noun minus Inflected Verb provided significant effects only when lowering the significance threshold ($p<0.001$, uncorrected); again, the effects were exclusively located in the left IFG. No significant differences were found in the subtraction Inflected Verb minus Infinitive Verb even at an uncorrected significance threshold, except for an effect in the left ventral IFG ($p<0.05$, uncorrected) (Table 2, Figure 5). Thus, signal change within left IFG, particularly in the ventral aspect, was somewhat modulated by the type of processes required in the naming of the same event: greatest for the Action Noun, intermediate for the Inflected Verb and least for the Infinitive Verb .

DISCUSSION

The results of our fMRI study provide evidence that naming an event relies on the activation of the left perisylvian cortex, the right temporal pole, and the right hippocampus, and that, within this system, the activity of the left IFG is greatest when the same event is named by action nouns, intermediate when it is named by inflected verbs, and least when it is named by infinitive verbs. In what follows, we will concentrate on the interpretation of differences between the three naming conditions, as revealed by the direct comparisons.

The dissociation observed in neuropsychological studies between noun and verb processing has been taken to support hypotheses that words from different grammatical classes engage different neural networks, by virtue of their grammatical properties (e.g., Caramazza & Hillis, 1991). However, the distinction between nouns and verbs largely co-occurs with semantic differences between these two types of words. Semantic differences between nouns referring to objects and verbs referring to actions has been linked to different neural substrates, with nouns preferentially engaging left inferior temporal cortices (e.g., Damasio *et al.,* 2004), involved in perceptual object recognition and verbs preferentially engaging left premotor cortex, left IFG and left MT, responsible for action processing (e.g., Perani *et al.,* 1999; Tranel *et al.,* 2005).

Previous studies investigating noun-verb processing have attempted to reduce the impact of the semantic confound using abstract words (Bedny, *et al.*, 2006; Perani *et al.,* 1999; Tyler *et al*, 2001; 2004; Shapiro *et al.*, 2006), or by comparing real words to pseudowords (Shapiro *et al*, 2005; 2006). However, as discussed in the introduction, these strategies set up to control for semantic correlates may not be ideal, because it cannot be excluded that, for example a pseudoword, is processed as object-like, when presented in a noun context and as event-like, when presented in a verb context.

In our study we eliminated the semantic confound by using only words referring to events. More precisely, we asked speakers to name the same event using either a noun or a verb. Grammatical class information was directly relevant to the task as we instructed participants to name the picture either as a noun or a verb. Thus, although speakers were producing single words, grammatical class information was relevant to the task and therefore this study is not susceptible to this criticism that can be, instead, be raised to some previous studies that failed to observe noun or verb-specific activations (e.g., Tyler *et al*., 2001; Vigliocco *et al.,* 2006).

In contrast to some previous studies (Perani *et al.,* 1999; Tyler *et al*., 2004), we failed to observe any verb specific activations. We found, instead, noun specific activations in left IFG, specifically in BA 44 and more ventrally in BA 45/47. Importantly, these noun-specific activations fall in close proximity to the verb-specific activations reported in the aforementioned studies. In our follow-up analysis, we further showed that the signal change in left ventral IFG show a trend toward being modulated by the processing differences across the three conditions. In particular, we found strongest activation for the Action Nouns, intermediate for Inflected Verbs and weakest for Infinitive Verbs. This finding clearly indicates that left IFG engagement is not selectively linked to verb processing. Rather, our finding suggests that left IFG is engaged in the combinatorial and selection processes required for producing an inflected form of a verb (that, as we described in the introduction can be considered as syntactic in addition to morphological processes) and, to a greater extent, in the processes engaged in producing derived word forms.

A number of previous studies have established a role for left IFG in syntactic and morphological processing during comprehension (e.g., Caplan *et al*, 2000; Cooke *et al*., 2006; Dapretto & Bookheimer, 1999; Gabrieli *et al*, 1998; Marangolo *et al*, 2004; Moro *et al,* 2001). The few studies that have investigated phrasal production have also reported activations related to phrasal production in left IFG. In experiments by Indefrey and colleagues (2004), speakers of German were presented with displays showing animated scenes and they were asked to describe them using full sentences (e.g., "The red square launches the blue ellipse"), sequences of phrases with local, but not sentence level syntactic structure (e.g., "red square", "blue ellipse", etc.) or sequences of words without any syntactic structure (e.g., "square", "red", "ellipse", etc.). It was found that a left IFG region, overlapping in part with BA 44, although mainly posterior to Broca's area (most likely in BA6) was most activated in the sentence condition, less active in the phrasal condition and least active in the word condition. Activations in left IFG (greater, however, in BA45 than in BA44) were also reported in the study by Haller et al (2005) in which German speakers were asked to produce sentences aloud (e.g., "The child throws the ball") in response to syntactically incomplete stimuli (e.g.," throws", "ball"; "child"), relative to the condition in which they were asked to read aloud the same words; or in which they were asked to read aloud corresponding sentences. What is common between these studies and our study is that the conditions in which left IFG activations are observed as ones where combinatorial and selection processes are engaged. A role for left IFG in integrating different types of linguistic information has been argued by researchers investigating sentence comprehension (Hagoort, 2005; Martin & Chao, 2001; Price, 1998).

It is noteworthy that two separate activation foci were found in left IFG. One could be localized on the basis of probability mapping in BA44, the other was approximately localized more ventrally in BA 45/47. There is extensive evidence for the fractionation between these components of the classical Broca's region, on the basis of cytoarchitectonic and hodological differences (Anwarder *et al.*, 2006; Petrides & Pandya, 2002). This structural distinction has been proposed to reflect a functional differentiation. It has been argued that the dorsal, 44/6 area is involved in the computation of local syntactic dependencies in word production and comprehension, while the ventral 45/47 area is linked to lexical/semantic processing (Friederici *et al.*, 2006; Indefrey *et al.*, 2004; Paulesu *et al.*, 1997; Poldrack *et al.*, 1999). Our study was not designed to test any specific hypothesis of differentiation within left IFG. It is, however, possible that whereas the graded effect we observed in dorsal IFG reflects to a greater extent the engagement of combinatorial and syntactic processes; the graded effect we found in ventral IFG might be linked to processes of selecting and selecting the lexical status of inflected and derived forms to-be-produced, these processes could be more demanding for derived than inflected words.

The processes recruited in producing Action Nouns may not be strictly linguistic (i.e., they may be domain general). In our study, when presented with pictures depicting actions, the most automatic naming response is to name the picture using a verb, and specifically an Infinitive verb in Italian. This can be established by simply presenting pictures to speakers and asking them to name them without giving them any more specific instructions regarding the form of the naming response. In order to name the same picture with an Action Noun speakers have to select a less favourite response instead. Thompson Schill has proposed that BA 44 plays a crucial role in conditions characterized by "high selectional demands" among competing alternatives (Thompson Schill *et al*, 1997). In our experiment, the Action Noun was the less favored response to the pictures as indicated by the fact that subjects were slower in producing Action Nouns than in all the other conditions (see Figure 2). Thus, it is plausible that Action Nouns posed the highest selection demands among competing alternatives in our experiment. Conspiring in rendering Action Nouns the least favorite response among our conditions, these words are also less frequent and are acquired later than the verbs. It has been shown in previous fMRI studies greater left IFG activations for low frequency than high frequency words (Fiebach *et al*., 2002; Chee *et al*., 2002).

In conclusion, our study demonstrates that words belonging to different grammatical classes (nouns and verbs) are not represented in segregated neural networks. Rather, neural segregation emerges as the result of other differences between nouns and verbs that are usually confounded with the grammatical class difference across languages. First, in most previous patient and imaging work, differences between nouns and verbs may have come about as a semantic difference between objects and actions. In previous studies that did not suffer of this confound, and in which morphological processes were not highly engaged, no verb-specific activations in left IFG was found (Vigliocco *et al*, 2006; Saccuman et al., 2006). In the present study we showed that if we control for semantic differences (asking participants to name only events and more specifically the same events as either noun or verb) and manipulate the extent of morphological processing across the grammatical class of verbs and nouns, left IFG activations are shown to be modulated by the complexity of the morphological processes involved and/or by the selection demands of the morphological task rather than being associate to verb-specific processing.

Thus, our results do call into question the view that grammatical class *per se* drives neural segregation within the language network at the lexical level restricting the role of this information in driving neural organization to its use in connected speech.

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Table 1. MNI stereotactic coordinates (in mm) for the significant activations in the main effect including all three experimental conditions (p<0.001, FWE corrected). CP, cytoarchitectonic probabilities (Amunts et al., 1999).

	x	y	z	Z score	CP
Left inferior frontal gyrus	-46	10	24	6.30	40% BA44
Left ventral premotor cortex	-54	4	38	Inf	
Left superior temporal gyrus	-52	-14	-6	6.48	
Left temporal pole	-44	2	-10	6.48	
Right temporal pole	44	2	-14	6.64	
R hippocampus	26	-34	2	6.77	

Table 2. MNI stereotactic coordinates (in mm) for the significant activations in the direct comparisons. CP, cytoarchitectonic probabilities (Amunts et al., 1999).

	x	y	z	Z score	CP
Action Noun – Infinitive Verb					
Left inferior frontal gyrus	-46	16	26	5.02	60% BA44
Left inferior frontal gyrus	-48	24	-4	4.67	
Action Noun – Inflected Verb					
Left inferior frontal gyrus	-46	16	26	4.24	60% BA44
Left inferior frontal gyrus	-48	24	-4	3.47	
Inflected Verb – Infinitive Verb					
Left inferior frontal gyrus	-48	24	-4	1.73	

Figure Captions

Figure 1. Examples of pictures used in the study along with naming responses required in the three different conditions.

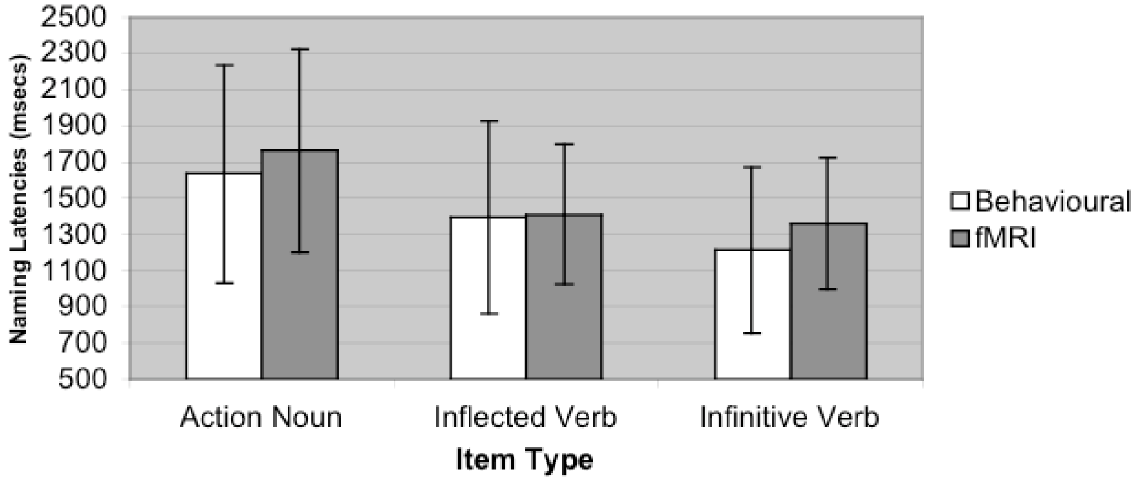
Figure 2. Mean naming latencies (in ms) for the three experimental conditions for 14 participants (Behavioural, Group 1) who performed the naming task outside the scanner and for the 12 participants (fMRI, Group 2) performing the task during scanning.

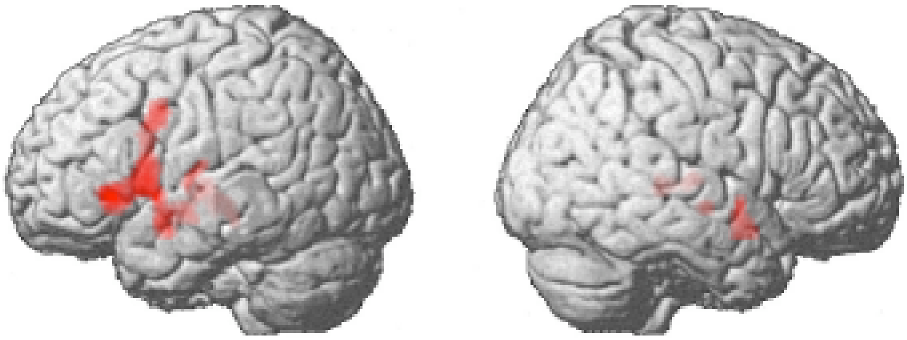
Figure 3. Standard SPM2 3D-rendering showing the significant activations for the main effect including all three naming conditions ($p<0.001$, FWE correction).

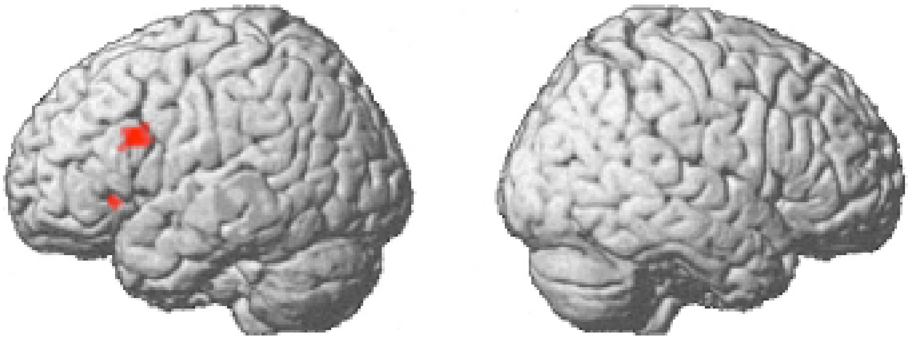
Figure 4. Standard SPM2 3D-rendering showing the significant activations for the direct subtraction Actions Noun minus Infinitive Verb ($p<0.05$, FDR correction).

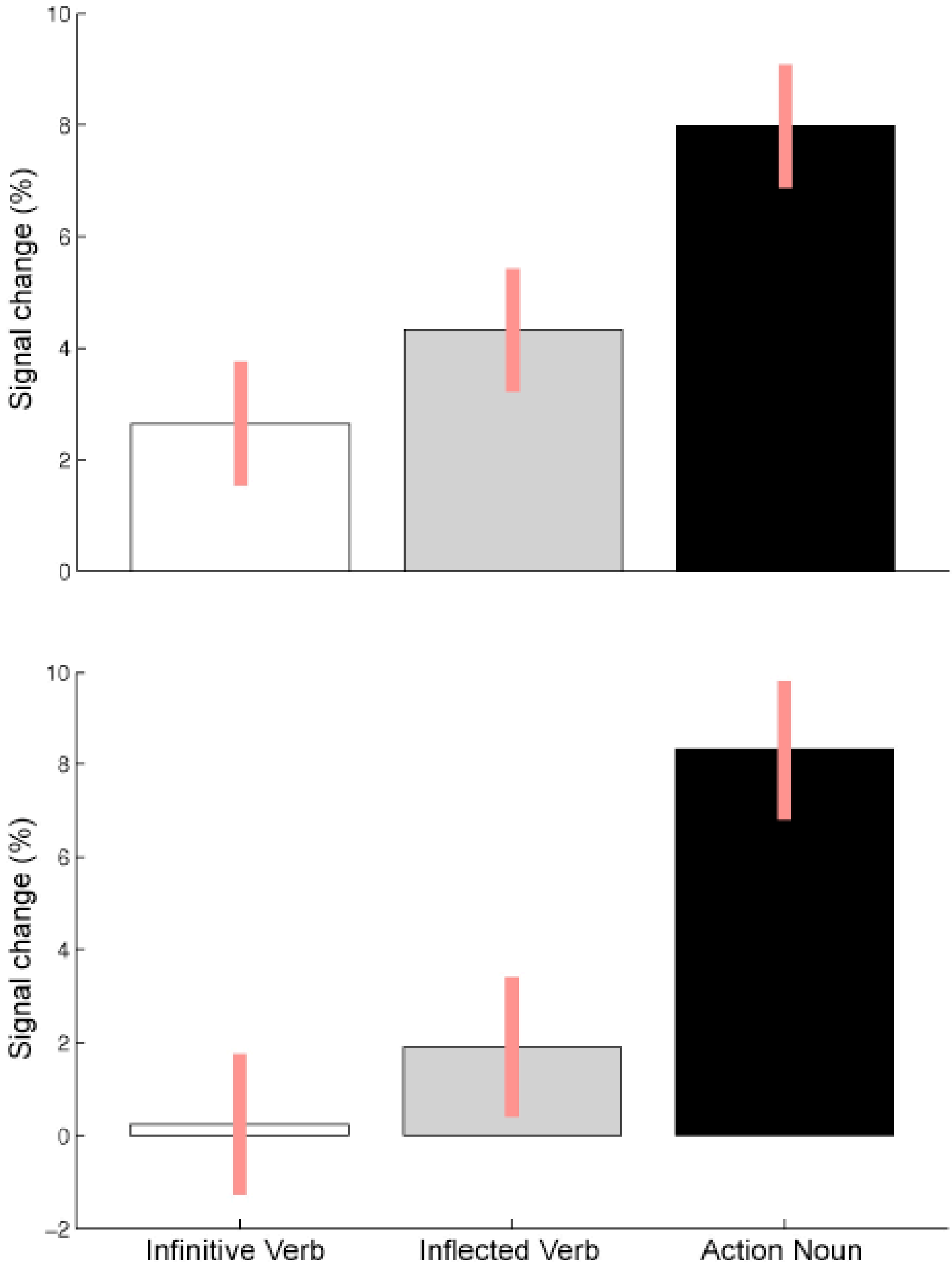
Figure 5. Histograms representing percent signal change and 90% confidence intervals in the three experimental conditions (Infinitive Verb: white; Inflected Verb: gray; Action Noun: black) in two different portions (dorsal vs. ventral) of the left inferior frontal gyrus (upper part: x=-46, y=16, z=26; lower part: x=-48, y=24, z=-4).

Picture	Infinitive Verb	Inflected Verb	Action Noun
	**Ballare** [to dance]	**Ballano** [(they) dance]	**Ballo** [the dance]
	**Leggere** [to read]	**Legge** [(she) reads]	**Lettura** [the readng]
	**Saltare** [to jump]	**Salta** [(he) jumps]	**Salto** [the jump]


2500
2300
2100
1900
1700
1500
1300
1100
900
700
500
Naming Latencies (msecs)
Action Noun
Inflected Verb
Infinitive Verb
Item Type
Behavioural
fMRI






Signal change (%)
10
8
6
4
2
0
Signal change (%)
10
8
6
4
2
0
−2
Infinitive Verb
Inflected Verb
Action Noun