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Morphological complexity reveals verb-specific prefrontal engagement

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ABSTRACT

Neuropsychological evidence and recent rTMS studies strongly suggest that damage or inhibition of left prefrontal areas may result in specific impairment of verb morphosyntactic processing. However, functional imaging studies have so far failed to identify an area specifically related to grammatical aspects of verb knowledge. To date very few functional studies have been conducted in languages other than English, a language with limited inflectional morphology. In the present study, we make the hypothesis that neuronal responses for verb grammatical processing may be more or less evident depending on the morphological complexity of verbs in a given language.

Exploiting the morphologically rich verbal paradigm typical of the Italian language we implemented an event-related functional MRI design to identify cortical regions that were active when subjects produced nouns or verbs in the context of short phrases. Results showed an area of verb-specific activation for real verbs in a small left frontal region corresponding to the intersection of BA10, BA46 and BA 47. We interpret the results as revealing that language-specific morphological properties may modulate the pattern of grammatical specific activations. Specifically, higher degrees of morphophonological complexity may engage a greater variety of morphophonological operations, thus enhancing the possibility of activations specific for a given grammatical class.

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1. Introduction

Dissociations between nouns and verbs have often been documented in the speech performance of patients with language impairments (Caramazza & Hillis, 1991; Damasio & Tranel, 1993; Daniele, Giustolisi, Silveri, Colosimo, & Gainotti, 1994; McCarthy & Warrington, 1985; Miceli, Silveri, Villa, & Caramazza, 1984). There is ongoing debate in the neuropsychological literature on whether these observations reflect truly grammatical distinctions or are simply a by-product of the kinds of meanings associated with prototypical nouns (objects) and verbs (actions). For instance, lesions involving higher-order visual association areas in the temporal lobe may give rise to a selective impairment for nouns by virtue of the fact that object words tend to be named as nouns. On the other hand, lesions involving premotor areas may give rise to a selective impairment for verbs by virtue of the fact that action words tend to be named as verbs (Bak, O'Donovan, Xuereb, Boniface, & Hodges, 2001; Luzzatti, Aggujaro, & Crepaldi, 2006). However, there are also patients whose noun/verb dissociation remains even in the absence of semantic problems (Berndt, Haendiges, Burton, & Mitchum, 2002; Crepaldi et al., 2006; Laiacona, Capitani, & Caramazza, 2003; Shapiro & Caramazza, 2003a; Shapiro, Pascual-Leone, Mottaghy, Gangitano, & Caramazza, 2001). These patients are usually unable to use words from the impaired grammatical class in the appropriate grammatical context. This observation is particularly striking in that it may concern noun-verb homonym pairs (e.g., *the play* vs. *they play*) or non-words used in noun or verb contexts (e.g., *the wug* vs. *they wug*). That is, there are patients whose performance changes dramatically depending on the context — nominal or verbal — in which phonologically identical materials appear.

Although suggestive, the neuropsychological evidence, on its own, has not allowed a systematic investigation of the neural correlates of noun and verb processing. Indeed, brain lesions are often extensive or non-uniform across patients who show similar impairments in performance, thus it is not possible to draw meaningful inferences about the supposed grammatical role of a given area. Supporting evidence has come from transcranial magnetic stimulation (TMS) that has shown that the ability to perform grammatical operations on verbs may be selectively disrupted following repetitive TMS (rTMS) of a well-defined portion of the left prefrontal cortex, just anterior and superior to Broca's area and clearly distinct from motor planning areas (Cappelletti, Fregni, Shapiro, Pascual-Leone, & Caramazza, 2008; Shapiro, Pascual, Mottaghy, Gangitano, & Caramazza, 2001). This finding reveals the importance of this area for verb morphosyntax (for further evidence, see Finocchiaro et al., 2008).

On the other hand, the picture that emerges from imaging studies is rather inconsistent in showing a verb-specific activation pattern. Indeed, some of these studies have found neural differences that depend on the general difficulty of a given linguistic operation rather than on the grammatical class (noun or verb) to which a given grammatical operation applies (e.g., Tyler, Bright, Fletcher, & Stamatakis, 2004). Other studies have observed a specific pattern of activation for verbs but only when inflected forms were used, suggesting that form class is not a first-order organizing principle underlying the representation of nouns and verbs as lexical entries (Longe, Randall, Stamatakis, & Tyler, 2007). In addition, where some attempt has been made to disentangle effects of semantic factors like concreteness from effects of grammatical category as such (e.g., Perani et al., 1999) spatially distinct patterns of activation unambiguously due to the grammatical aspects of noun and verb knowledge have not been found. Finally, there are also studies that have found activation of areas usually associated with different semantic aspects of verbs and nouns (Bedny, Caramazza, Grossman, Pascual-Leone, & Saxe, 2008), even when the task emphasized the grammatical component and minimized the semantic impact (e.g., producing non-words used in verb or noun contexts, see Shapiro, Moo, & Caramazza, submitted for publication).

What is remarkable from this brief review of the imaging literature on nouns and verbs, is that the puzzling negative finding to date extends to both comprehension and production studies, and also to studies where tasks that specifically tapped subjects' grammatical knowledge about words were employed. One aspect common to many of these studies is that they based their observations on one language, English. This may be an important limitation given that English has limited inflectional morphology. Nouns may only be specified for number (singular vs. plural), whereas in many other languages they also encode grammatical gender and case. Similarly, English regular verbs make few distinctions within a given paradigm: they only have three synthetic forms (e.g., *walk*, *walks*, *walked*),

with the other forms derived through analytic processes by combining an auxiliary with the base form of a given verb (e.g., *will walk*; *would walk*) or by emphasizing the nominal component (e.g., *walking*). Thus, grammatical tasks in English may engage highly routinized processes, eventually leading to a reduced neural engagement of the areas related to verb and noun grammatical processing.

In Italian, verbs may belong to three different conjugation classes, and different forms are used depending on tense, person, and number features, so that greater neural engagement may be expected compared to English. Still, those few imaging studies that have been conducted in Italian have not found a noun/verb difference that could be unambiguously attributed to grammatical rather than semantic aspects of word knowledge. We suggest that this failure could be attributed to methodological reasons. For instance, Perani et al. (1999) used a lexical decision task that even in carefully designed studies, may not be sufficiently engaging to reveal differences unambiguously due to grammatical class. On the other hand, Siri et al. (2008) included deverbal nouns in their noun set, and this could have introduced an undesirable verbal component in the processing of nouns, thus leading to an underestimation of the grammatical noun/verb contrast.

We make the hypothesis that a language with a rich verbal paradigm may offer greater opportunity to observe verb-specific activations because its higher degrees of morphophonological complexity will necessarily engage a greater variety of morphophonological operations. Thus, we suggest that, in order to maximize the possibility of detecting a grammatical effect, it is important to choose a task that specifically taps on verbs' and nouns' morphosyntax.

To summarize, our hypothesis predicts that the use of an explicit morphosyntactic task in Italian, a language with a morphologically rich verbal paradigm, may allow us to observe a verb-specific activation within the left inferior and middle frontal gyrus. This anatomical prediction is based both on neuropsychological and rTMS findings that suggest a specific involvement of the left frontal cortex in verb morphosyntax.

2. Methods

2.1. Participants

Sixteen healthy right-handed subjects were recruited. Two of them were excluded because of excessive movement revealed by data preprocessing. Thus, the experimental sample was composed by fourteen subjects (7 males and 7 females, mean age 36.6 years, range 20–51). All participants were native speakers of Italian with no history of neurological or psychiatric disorders. Handedness was assessed using the Edinburgh Inventory (Oldfield, 1971). The study was approved by the Ethics Committee of the University of Trento and all participants signed an informed consent form.

2.2. Materials

Stimuli consisted of 36 regular verbs, 36 regular nouns and 36 pseudo-words used as nouns or verbs. The pseudo-words were generated by changing one or two phoneme(s) of real words not used in the experiment. The gender of pseudo-nouns was established on the basis of the high correlation between the ending of the noun and its gender (/-o/nouns are usually masculine and /-a/ nouns are usually feminine). Thus, only pseudo-nouns ending in /-a/ or /-o/ were selected as experimental stimuli so that participants could choose the "correct" determiner or quantifier form. Pseudo-nouns and pseudo-verbs were matched for number of neighbors (i.e., the number of real words phonologically related to a given pseudo-word), the frequency of the neighborhood (i.e., the mean frequency of the real neighbors), and the frequency of the most frequent real neighbor. Real verbs and nouns were divided into two different semantic categories of 18 items each: "action" and "non-action". Real words were matched for length and cumulative frequency across the four sets. Nouns and verbs were also matched for the surface frequency of the forms used within each grammatical class. Frequency counts were based on the corpus COLFIS (http://alphalinguistica.sns.it/BancheDati.htm).

Given that there is a high correlation between action and imageability, it was impossible to balance imageability across the four word sets. However, Likert ratings (1 = very low imageability, 7 = very high imageability) from 10 pilot subjects showed that there was no difference in imageability between

nouns and verbs within each semantic category. Furthermore, the difference in imageability between action and non-action words was comparable for nouns and verbs.

2.3. Task procedure

Participants were presented with verb or noun phrases containing real nouns (e.g., *uno starnuto* 'a sneeze'; *molti starnuti* 'many sneezes') and verbs (e.g., *io taglio* 'I cut'; *tu tagli* 'you cut') or pseudo-words used as nouns (e.g., *un poffio; molti poffi*) or verbs (e.g., *io blimo; tu blimi*).[1] The phrase was displayed for 1 s, and then followed by a cue stimulus (*uno…/molti…* 'one…/many…' for nouns, *io…/tu…* 'I…/you…' for verbs) for 1 s; the cue instructed participants on the morphological form to be produced for the preceding noun or verb. Participants were instructed to read the phrase silently and to produce the correct noun or verb form according to the cue. The next trial started at a jittered interval between 2 and 12 s after the disappearance of the cue. Half of the trials required the subject to make a morphological transformation of the stimulus; the other half of the trials did not require any transformation. A training session of eleven additional phrases (with 3 verbs, 3 pseudo-verbs, 3 nouns, and 2 pseudo-nouns) was preformed outside the scanner and inside the scanner immediately before starting the experiment.

2.4. Imaging data acquisition

An event-related design was implemented to present all the trials ($N = 216$) during a single run. A genetic algorithm (Wager & Nichols, 2003) was used to optimize the experimental design so that maximum statistical power could be achieved, and allowed to generate eight different randomizations. Each subject was assigned to a given randomization according to a Latin-square design. The total duration of the run was approximately 21 min. E-Prime software (Psychological Software Tools, Pittsburgh, PA) was used to present the stimuli. During the scanning sessions, vocal responses were monitored using a fiber optic audio system. Brain images were collected with a 4-T Bruker MedSpec scanner (Bruker Inc., Ettlingen, Germany) using an 8-channel head coil. Subjects wore ear plugs and headphones and viewed stimuli projected onto a screen via an angled mirror attached to the head coil.

Functional images were acquired using a T2*-weighted gradient-echo echo-planar sequence (repetition time = 2200 ms, echo time = 33 ms, flip angle = 75°, acquisition matrix = 64 × 64, slice thickness = 3 mm, inter-slice gap = 0.45 mm, field of view = 192 × 192 mm, number of slices = 37). The functional run had 569 brain volumes. For subsequent superposition of functional statistical parametric maps, a high-resolution structural 3D inversion recovery T1-weighted volume was acquired (repetition time = 2700 ms, echo time = 4.18 ms, inversion time = 1020 ms, flip angle = 7°, acquisition matrix = 256 × 224, slice thickness = 1 mm, field of view = 256 × 224 mm, number of slices = 176).

2.5. Imaging data analysis

Preprocessing and data analysis were conducted using BrainVoyager QX 1.9 software package (Brain Innovation, Maastricht, The Netherlands). Functional images from each subject were corrected for slice time acquisition with cubic spline interpolation. The first two volumes were discarded. All volumes were realigned using a 3D rigid-body spatial transformation. Temporal filtering included linear trend removal and a 0.017-Hz high pass filter. The functional data were co-registered to structural images and then spatially smoothed using a Gaussian kernel (full width at half maximum = 4 mm). The structural and co-registered functional data were normalized into standard stereotaxic space (Talairach & Tournoux, 1988).

The time course of the estimated translation and rotation parameters on *x*, *y*, *z* axes were inspected and maximum values were computed for each subject. A correlation analysis was performed between each movement parameter estimation and a regressor modeling the onset of the speech response of the subject. The average maximum head translation and rotation across subject was 0.98 mm and 1.0 deg respectively, with no subject exceeding 3 mm and 2.5 deg. No significant correlation between any movement parameter and the onset of speech response was found.

[1] Technically speaking, verb phrases are formed by the verb and its object, if present. However, for the sake of simplicity, the label "verb phrase" will refer to the cluster formed by the subject pronoun and the verb throughout the paper.

A regressor for each trial type ($N = 12$) was created. Each regressor was convolved with a standard hemodynamic response function. The regressors of all subjects were used to implement a multi-subject general linear model (GLM) random effect analysis. Moreover, in order to remove any possible confounds due to correlation of BOLD signal variation with movement, the movement parameters were included as no-interest covariates. We defined four factors: *Grammatical Class* (nouns/verbs); *Lexical Status* (word/pseudo-word), *Morphological Transformation* (yes/no) and *Semantic Category* (action/non-action). The beta maps obtained from the GLM analysis were entered into two separate repeated measures ANOVAs, each comprising 3 factors: [*Grammatical Class* × *Lexical Status* × *Morphological Transformation*] and [*Grammatical Class* × *Semantic Category* × *Morphological Transformation*]. The main reason to perform two separate ANOVAs was that one factor, namely the Semantic Category, could not be applied to pseudo-words. The resulting statistical parametric maps were corrected using a cluster-size threshold extrapolated with a 3D extension of the randomization procedure described by Forman et al. (1995). First, a voxel-level threshold uncorrected for multiple comparisons was set at $p < 0.01$ or $p < 0.001$. The maps were then subjected to a whole-brain correction criterion based on an estimate of the map's spatial smoothness and on a Monte Carlo simulation (1000 iterations) for estimating cluster-level false positive rates. The cluster-size threshold that yielded a cluster-level false positive rate (α) of at least 0.05 was then applied to the statistical parametric maps.

The Talairach Client software (Lancaster et al., 2000) was used to assign Talairach Atlas labels for a given *x*, *y*, *z* coordinate, represented by the center of gravity of each activation.

3. Results

The average accuracy across subjects was 97.6% (±4.3). No subject reported any difference in difficulty among the different trial types.

The factor *Grammatical Class* was explored in both ANOVAs.

In the first ANOVA, compared to verbs and pseudo-verbs, nouns and pseudo-nouns elicited a greater activation bilaterally in visual areas close to the calcarine fissure (BA18) and within the left fusiform gyrus (BA19). No significant activation was observed using the opposite contrast. The second ANOVA, where pseudo-words were excluded because the action/non-action distinction does not apply, confirmed a greater activation in occipital areas for nouns. More interestingly, it also revealed a greater activation for verbs in a small left frontal area located in the posterior portion of the middle frontal gyrus, at the border between BA10 and BA46, and in the dorsolateral portion of the right superior frontal gyrus, at the border between BA6 and BA8 (Fig. 1, Table 1).

Significant interaction between *Grammatical Class* and *Morphological Transformation* was found in many areas as displayed in Table 2. Post-hoc *t*-tests revealed that, when a transformation was required, in all areas nouns and pseudo-nouns were associated with greater activity with respect to verbs and pseudo-verbs. On the contrary, when no transformation was required, verbs and pseudo-verbs were associated with greater activity compared to nouns and pseudo-nouns. We did not find any area displaying a differential activation for verbs and pseudo-verbs depending on transformation, while all areas reported in Table 2 showed greater activation for nouns and pseudo-nouns when a transformation was required compared to when no transformation was required.

In line with these results, time course inspection in all these areas demonstrated a constant activation for verbs and pseudo-verbs independently from transformation, while a differential activation was present for nouns and pseudo-nouns. Fig. 2 shows examples of time course activation in the left inferior frontal gyrus (BA44), at the border of the left inferior/superior parietal lobule (BA40/7) and in the posterior part of left superior temporal gyrus (BA22).

The interaction between *Grammatical Class* and *Lexical Status* was found bilaterally in the middle third of the lateral portion of the precentral gyrus (BA4/BA6) and in the superior lateral portion of the right cerebellar hemisphere (Table 2). In the bilateral precentral gyrus, increased activation was found for nouns compared to pseudo-nouns; in the right cerebellar hemisphere, increased activity was associated with pseudo-verbs when contrasted with real verbs.

No significant interaction was evident between *Grammatical Class* and *Semantic Category*.

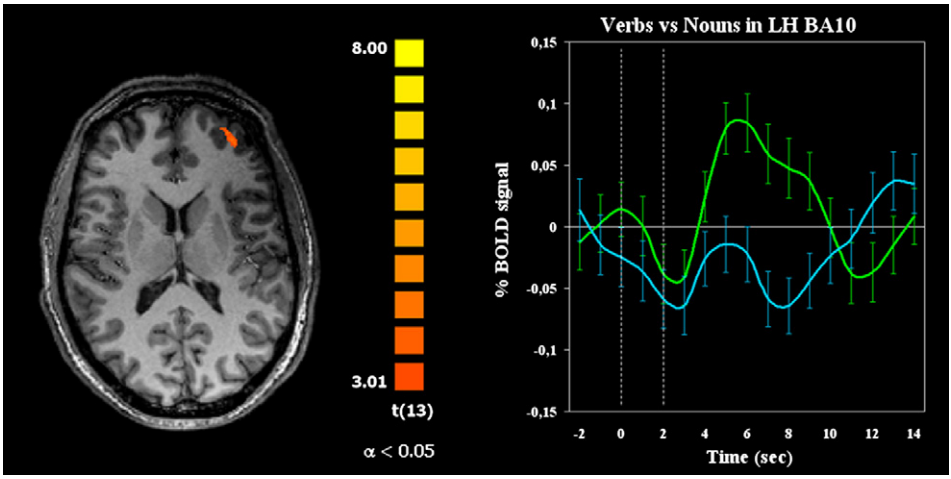

Fig. 1. Area in the left middle frontal gyrus (BA10) showing greater activation for verbs *vs.* nouns. The graph depicts the average percentage signal variation of all voxels in the region for verbs (green line) and nouns (blue line); the vertical lines indicate the start and the end of the trial. Vertical bars indicate the standard error of the mean value across subjects. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

The aim of this study was to look for a verb-specific pattern of activation in a language, Italian, with a morphologically rich verbal paradigm. We used a grammatical task which required participants to produce the correctly inflected form of nouns, verbs and pseudo-words used as nouns or verbs.

The comparison between real nouns and verbs showed an area of verb-specific activation located in the posterior portion of the middle frontal gyrus, at the intersection of BA10, BA46 and BA47, in a region lying between the most anterior portion of the dorsolateral prefrontal cortex (DLPFC) and the most posterior and dorsal portion of the anterior prefrontal cortex (aPFC). Most interestingly, this area is within the region that has been targeted in previous rTMS studies, in which it has been shown that inhibitory rTMS to the left anterior midfrontal gyrus selectively interferes with verb production (Cappelletti et al., 2008; Shapiro et al., 2001).

As in other studies, we found many brain areas activated during the processing of verbs and nouns (Longe et al., 2007; Perani et al., 1999; Shapiro, Moo, & Caramazza, 2006; Siri et al., 2008; Tyler et al., 2004). For instance, we found that the left inferior frontal gyrus, the parietal lobe, and the posterior superior temporal gyrus are activated when verbs are processed (Shapiro et al., 2006). However, in our

Table 1
Grammatical class effects.

Area	Talairach coordinates			Vol (mm^3)	*T* value (max)	BA
	x	*y*	*z*			
Verbs > nouns						
RH superior frontal gyrus	28	17	44	419	5.23	8
LH middle frontal gyrus	−31	45	7	205	5.07	10
Nouns + pseudo-nouns > verbs + pseudo-verbs						
RH Lateral lingual gyrus	14	−82	−6	943	8.92	18
LH Fusiform gyrus	−26	−78	−16	472	8.25	19
Bilateral cuneus	−1.5	−73	12	3100	9.08	18

Cluster level corrected $\alpha < 0.05$ Abbreviations: RH = Right Hemisphere; LH = Left Hemisphere; Vol = cluster volume; BA = Brodmann Area.

Table 2
Summary of results for interaction between *Grammatical class*, *Morphological transformation*, and *Lexical status*.

Area	Talairach coordinates			Vol (mm^3)	*F* value (Max)	BA
	x	*y*	*z*			
Grammatical class × Transformation interaction						
RH Precentral gyrus	50	−12	31	5128	59.01	6
RH Superior temporal gyrus (posterior part)	48	−37	6.1	777	88.23	22
RH Thalamus	11	−17	7.6	439	85.59	
LH Precentral & inferior frontal gyrus	−44	−9.4	34	10 916	194.31	9/6/44
LH Middle occipital gyrus	−28	−89	−2.4	762	59.09	19
LH Inferior parietal lobule	−33	−50	43	640	56.2	40/7
LH Fusiform gyrus	−40	−62	−9.1	1862	82.84	37
LH Superior temporal gyrus	−44	−41	11	1628	62.09	41
LH Superior temporal gyrus (posterior part)	−53	−16	3.3	531	61.22	22
LH Insula	−29	17	10	760	49.45	13
LH Thalamus	−9.7	−18	8	407	47.16	
Bilateral Medial frontal gyrus	0.96	−0.62	52	4774	81.05	6
Grammatical class × Lexical status interaction						
RH Precentral gyrus	50	−11	36	476	54.72	4/6
LH Precentral gyrus	−42	−16	37	827	60.29	4/6
Right Superior lateral cerebellar hemisphere	38	−63	−21	506	50.81	

Cluster level corrected $\alpha < 0.05$. Abbreviations: RH = Right Hemisphere; LH = Left Hemisphere; Vol = cluster volume; BA = Brodmann Area.

study, morphological transformation strongly modulated the activity in this fronto–temporo–parietal network, as revealed by the significant interaction between transformation and grammatical category: a constant activation in those areas was obtained for verbs independently of the morphological operation required, whereas the activation associated with nouns was modulated by the morphological transformation.

Notably, the area of verb-specific activation found here has not been reported in previous neuroimaging data (Longe et al., 2007; Perani et al., 1999; Shapiro et al., 2006; Siri et al., 2008; Tyler et al., 2004). This area, however, should be expected to be activated based on neuropsychological and rTMS studies (Cappelletti et al., 2008; Shapiro et al., 2001). As suggested in the Introduction, the negative fMRI finding on nouns and verbs to date may be due to either the employment of tasks that were not enough grammatically demanding, or the use of a morphologically impoverished language – English. We argued in the Introduction that, since English has a rather impoverished morphology, a simple morphological alternation task can become "automatized" very early. On this view, participants could perform a task on verb morphology by routine procedures with minimal involvement of morphological processes and with minimal recruitment – invisible to the BOLD signal – of the areas deputed to those processes. On the other hand, our results show that, when using a language, like Italian, with a sufficiently rich verbal morphology, a simple morphological task such as the one used here cannot be performed without the recruitment of morphological areas that are specific for verbs, presenting a pattern of activation in convergence with all the rTMS studies that have been conducted on the topic.

Alternatively, one could argue that the verb-specific activation found here is only indirectly related to the morphological complexity of Italian verbs. In fact, among the roles associated with the anterior prefrontal cortex (aPFC) – the region within which we found a verb-specific activation, there is monitoring and manipulation of information within working memory (Petrides, 2005; Ramnani & Owen, 2004). These cognitive processes are required for the task used in our study. Although the same processes are supposed to be involved for all type of items, one possibility is that verbs are associated with increased need for performance monitoring. If this were the case, one would expect a certain amount of activity within the same area also for nouns. However, this area appears to be specifically active for verb processing and does not appear to be involved when nouns are processed. Thus, the noun/verb difference can hardly be attributed to a differential load in the cognitive processes that have been supposedly associated to the aPFC (Petrides, 2005; Ramnani & Owen, 2004).

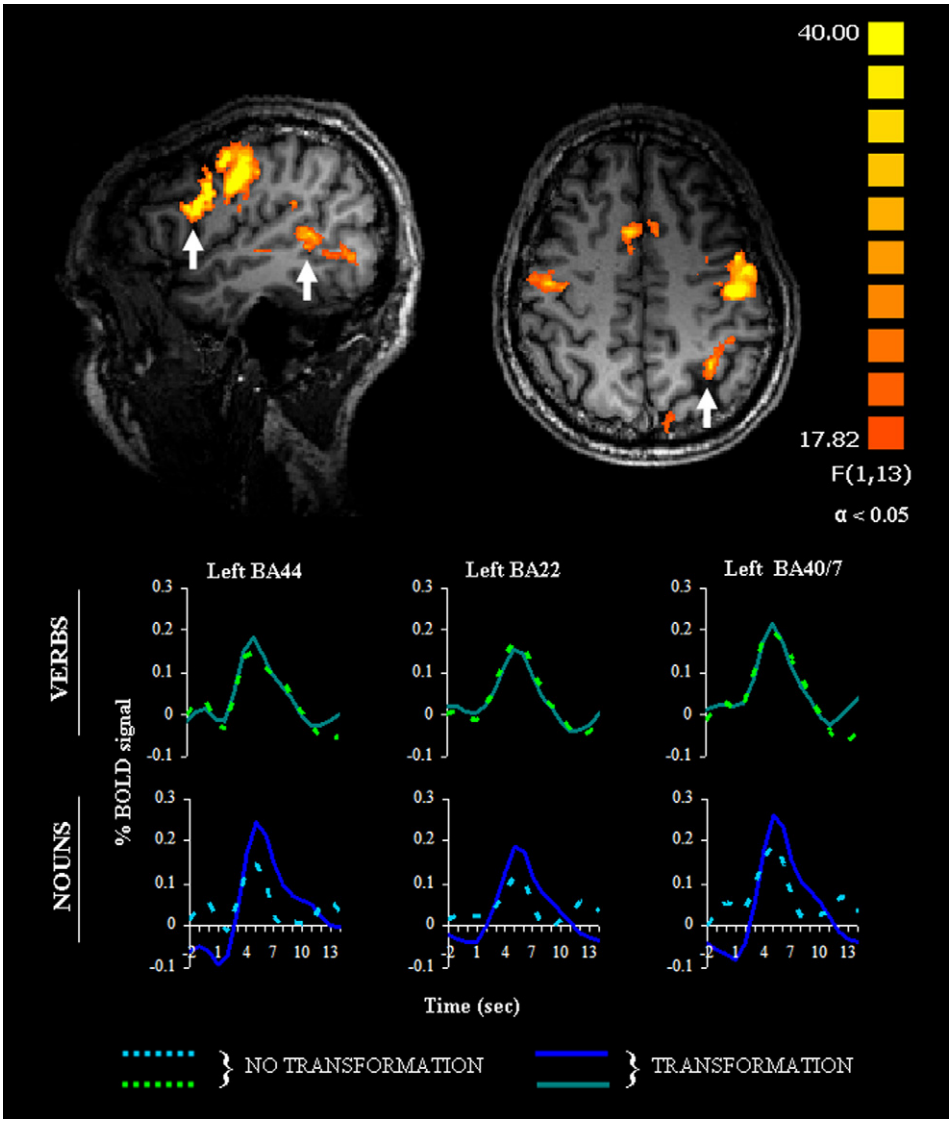

Fig. 2. Statistical parametric map of the F contrast displaying areas with a significant interaction between *Grammatical Class* and *Morphological Transformation*. The graphs depict the average percentage signal variation of all voxels for verbs (upper row) and nouns (lower row) from the left area BA44 and BA22, indicated by white arrows on the sagittal section, and left BA40/7 indicated by a white arrows on the axial section.

The greater activation that we found for nouns and pseudo-nouns in the occipital cortex is consistent with previous neuroimaging studies that investigated brain differences in grammatical processing of nouns and verbs in English (Shapiro et al., 2006; Tyler et al., 2004). However, both neuropsychological and neuroimaging studies overall do not allow a clear prediction about which brain area(s), if any, should be specifically involved in processing nouns as grammatical objects (see Shapiro & Caramazza, 2003b). Our data cannot shed new light on this question since the nominal paradigm in Italian is quite simple: Italian nouns are specified for grammatical gender (masculine vs. feminine), but, as in English, there are only two possible forms for each noun depending on the number feature

(singular vs. plural). Thus, we cannot attribute a definite role to the occipital activation found in the present study for nouns.

Perhaps the most challenging finding in this research concerns the failure to observe a verb-specific activation for pseudo-verbs. When the verb/noun contrast was analyzed with the inclusion of pseudo-words, no verb specific activation emerged. This finding may cast serious doubts on the grammatical explanation of the verb-specific activation for real verbs. In fact, it is generally agreed on that an effect to be considered grammatical should hold for both real words and pseudo-words used in the same grammatical context as the real words. The tacit assumption behind this idea is that pseudo-words are exactly the same as real words for the grammatical aspects, provided that they are used in the appropriate grammatical context. On the basis of our result, one could then argue that the verb-specific activation found here does not reflect the grammatical processing associated to verbs but some other aspects related to verb processing. One could also move further and say that there may not be a verb-specific region in the brain, and that the brain needs not to be organized around linguistic categories. Although the latter possibility cannot be definitely dismissed, we do not think that it is on the right track. The main evidence comes from neuropsychological studies that have repeatedly shown the existence of Noun/Verb dissociations. There are patients whose ability on a given grammatical class is selectively impaired even in the absence of semantic problems and even if the two sets of words (Nouns and Verbs) are carefully matched on the most relevant semantic variables and contain the same phonological material (e.g., *play* in *the play* vs. *they play*). For those patients, the dissociation remains also when pseudo-words used as nouns or verbs are employed instead of real words (see Introduction for some neuropsychological studies). With this general observation in mind, let us come back to our basic finding. In fact, one could acknowledge that the grammatical category may be an important organization principle of language in the brain, but still be skeptical about the grammatical account of the verb-specific activation found here. First, we should ask what the origin of the verb-specific activation found here could be if it is not grammatical. Usually, semantics is considered a good candidate as an account for an effect limited to real words. The reason is that since pseudo-words do not have a real semantics, a semantic effect is expected to be constrained by the lexical status of the stimuli. That is, it is not expected to extend to pseudo-words. Note, however, that the verb-specific activation found here is not modulated by the semantic category (action vs. non-action) of the stimuli, despite the fact that the action/non-action contrast has been proven to give rise to different activation patterns (Kaplan & Iacoboni, 2007; Khader, Jost, Mertens, Bien, & Rosler, 2010; Noppeney, Josephs, Kiebel, Friston, & Price, 2005; Oliveri et al., 2004). Second and more importantly, the verb-specific activation found here is within the region that recent rTMS studies have proven to be crucial for verb grammatical processing (Cappelletti et al., 2008; Finocchiaro et al., 2008; Shapiro et al., 2001). Of course, one could argue against the grammatical account also for those rTMS studies. This position, however, would be hard to defend. Indeed, those rTMS studies carefully controlled for the semantic aspects of the stimuli, and found a verb-specific effect for both real verbs and pseudo-verbs, thus supporting the grammatical account. There is an important difference, however, between previous rTMS results and the fMRI results of the present study: whereas in previous rTMS studies (Cappelletti et al., 2008; Shapiro et al., 2001) verbs and pseudo-verbs were both affected by rTMS to the anterior prefrontal cortex, in the present study the verb-specific activation only concerned real verbs and not pseudo-verbs.

In what follows, we will try to provide an explanation of the contrasting verbs/pseudo-verbs results found here in keeping with the grammatical account. This explanation would also account for why verbs and pseudo-verbs showed the same pattern in previous rTMS studies but not here.

We suggest that the contrast has to do with a fundamental characteristic of pseudo-verbs. As non-existing words, pseudo-verbs do not have a set of forms that may eventually become activated when participants perform a grammatical operation. This is especially true in the case of the present experiment, where the conjugation class, which determines the ending of many verbal forms, cannot be inferred from the two forms that are part of the response set. Indeed, all the Italian verbs take the same ending in those forms (I sg.: /*-o*/; II sg: /*-i*/), independently of the conjugation class to which they belong. However, it is necessary to know the endings of the infinitive form, which in Italian are /*-are*/, /*-ere*/, or /*-ire*/, in order to know the verb conjugation class and to consequently activate the full range of possibilities that characterize every existing verbal paradigm in Italian. For real verbs, participants know the conjugation class, so that the full morphological paradigm may become active as they

perform the grammatical task used here, leading to the recruitment of morphosyntactic areas that are specific for verbs. For pseudo-verbs, we did not specify a conjugation class. Thus, pseudo-verbs were not associated with a full paradigm and the consequent recruitment of neural structures devoted to verb morphosyntactic processes. Differently from Italian verbs, English verbs have a poor morphological paradigm that does not change depending on conjugation class. This means that it is always possible to infer a regular paradigm from a pseudo-verb stem. Thus, English speakers may activate the full paradigm of verbs and pseudo-verbs when doing a morphological transformation task. As a consequence, verbs and pseudo-verbs would involve the same area in the left anterior prefrontal cortex supposedly dedicated to grammatical processes (that is, what emerges from rTMS studies). However, in both cases, the procedure is so simple and the paradigm so restricted that the task may become routinized very early, thus leading to a reduced neural engagement of the areas related to verb processing, invisible to the BOLD signal. Hence, the failure of fMRI studies conducted in English to consistently get verb-specific activations independently from semantic aspects of verb knowledge.

At a more speculative level, another possible account for the failure to get verb-specific activation for pseudo-verbs here may be cast in terms of functional connections. On this view, the left frontal area, corresponding to the intersection of BA10, BA46 and BA47, would be activated for verb morphological processing as part of a circuit that also depends on lexical information. The argument here goes as follows. Pseudo-verbs, as non-existing words, are not listed in the lexicon. Then, if the lexical mediation is crucial for the activation of the relevant area, they cannot show activation in that area, no matter the morphological operation required.

In conclusion, our results show that there is a region of verb-specific activation that is most plausibly associated with verb grammatical processing. Most importantly, the verb-specific activation found here is within the region that has been shown to be dedicated to the grammatical processing of verbs on the basis of all the rTMS studies that have been conducted on the same topic. This is the first fMRI study in which the apparent contrast between rTMS and fMRI studies in the identification of a region selectively sensitive to verb morphosyntax has been reconciled. We believe that this was possible thanks to the use of a language with a rich verbal paradigm and a task that explicitly tapped on verbs' and nouns' morphosyntax. At a more general level, our results suggest that it is often crucial to pay greater attention to cross-linguistic differences in order to reveal the general principles that govern the neural representation of linguistic processes.

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