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Grammatical Categories in the Brain: The Role of Morphological Structure

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The current study addresses the controversial issue of how different grammatical categories are neurally processed. Several lesion-deficit studies suggest that distinct neural substrates underlie the representation of nouns and verbs, with verb deficits associated with damage to left inferior frontal gyrus (LIFG) and noun deficits with damage to left temporal cortex. However, this view is not universally shared by neuropsychological and neuroimaging studies. We have suggested that these inconsistencies may reflect interactions between the morphological structure of nouns and verbs and the processing implications of this, rather than differences in their neural representations (Tyler et al. 2004). We tested this hypothesis using event-related functional magnetic resonance imaging, to scan subjects performing a valence judgment on unambiguous nouns and verbs, presented as stems ('snail, hear') and inflected forms ('snails, hears'). We predicted that activations for noun and verb stems would not differ, whereas inflected verbs would generate more activation in left frontotemporal areas than inflected nouns. Our findings supported this hypothesis, with greater activation of this network for inflected verbs compared with inflected nouns. These results support the claim that form class is not a first-order organizing principle underlying the representation of words but rather interacts with the processes that operate over lexical representations.

Keywords: fMRI, inflection, noun, stem, verb

Introduction

Understanding and producing language require both rapid access to word representations and the ability to combine words in appropriate ways to express and decode utterances. A fundamental assumption of psycholinguistic theories is that these processes of syntactic combination require the grammatical category of each word to be coded in some way in the language system, so that combinatorial processes can operate over them appropriately. This crucial role for grammatical category information prompts the question—what are the cognitive and neural bases for distinctions between categories such as nouns and verbs, adjectives and adverbs?

Whether, and how, grammatical category information is neurally represented remains a contentious issue. Most research on the neural representation of words has focused on one specific category—nouns—and in most cases on a specific subset, namely, concrete nouns (e.g., Vandenberghe et al. 1996; Kiehl et al. 1999; Grossman et al. 2002; Sabsevitz et al. 2005). Considerably less attention has been paid to verbs, even though the roles of nouns and verbs in sentence interpretation and production are very different. Whereas verbs are essentially relational, binding actors, agents, and actions; nouns have a more referential role (Gentner 1981; Langacker 1987; Bock and Miller 1991). These differences in function between nouns and verbs have raised the issue of whether they have different neural substrates. This issue has largely been addressed by means of neuropsychological studies with brain-damaged patients who show dissociations between noun and verb deficits (e.g., Goodglass et al. 1966; McCarthy and Warrington 1985; Bates et al. 1991). In some cases, these have been linked to damage to distinct cortical regions, with verb deficits associated with left frontal damage and noun deficits associated with damage to temporal cortex (Goodglass et al. 1966; Damasio and Tranel 1993; Daniele et al. 1994). However, this is not a consistent pattern. Some patients who show disproportionate deficits for nouns have frontal damage and others who have verb deficits do not have accompanying frontal damage (Shapiro et al. 2000).

Several hypotheses have been proposed to account for the grammatical category dissociations observed in neuropsychological patients. One type of account claims that noun/verb dissociations are reducible to semantic factors—for example, nouns and verbs typically differ in terms of imageability (e.g., Marshall, Chiat et al. 1996; Marshall, Pring et al. 1996; Bird et al. 2000). Another type of account exploits the fact that nouns and verbs differ in the morphological processes that operate over them; for example, in English, verbs are inflected to mark number, tense, and person (e.g., 'he walks, he walked, they walk'), whereas nouns are only inflected for number ('1 dog/2 dogs'). Thus, it has been suggested that for some patients noun/verb dissociations may stem from differing abilities to carry out these morphological operations (Shapiro et al. 2000; Tyler et al. 2004). Finally, lexical accounts claim that grammatical category information is represented in the mental lexicon for each word form (independent of semantics). The lexicon is therefore organized along grammatical boundaries such that a lesion can selectively impair the ability to retrieve word forms within one category. This account is supported by findings of modality-specific deficits, in which a patient has difficulty in producing verbs in, for example, speech but not writing (Hillis et al. 2002; Rapp and Caramazza 2002). Such a deficit is claimed to occur at the level of modality-specific word forms and could not be explained by a semantic deficit which should affect all modalities equally. Although the neuropsychological data are not fully consistent with any of these accounts, they are not necessarily mutually exclusive (Shapiro and Caramazza 2003). Grammatical category distinctions may be reflected at multiple levels of the linguistic system—semantic, lexical, and morphological. They may also support representational (e.g., fractionation of form-based lexica along grammatical category lines) and processing (e.g., triggering distinct morphological computations) differences.

One of the limitations of relying too heavily upon neuropsychological studies is that descriptions of a patient's behavioral data are not always accompanied by detailed information about the location and extent of their lesion, making it difficult to unequivocally associate behavior and damage. This, plus the fact that patients often have extensive lesions that encompass many cortical regions, highlights the importance of obtaining data from unimpaired individuals in neuroimaging studies. Unfortunately, neuroimaging studies of grammatical category distinctions do not present a consistent picture. Whereas some studies show that nouns and verbs are associated with activation in different cortical regions (Perani et al. 1999; Shapiro et al. 2005), others claim that there is no evidence for neural differentiation as a function of grammatical category (Warburton et al. 1996; Buckner et al. 2000; Li et al. 2004). These inconsistent results may be due to differences among the language, tasks, materials used, and whether factors such as morphological structure and semantic variables have been sufficiently controlled. In previous neuroimaging studies, using both lexical decision and semantic categorization tasks, we have shown that nouns and verbs activate the same left-lateralized regions (inferior frontal gyrus [IFG] and temporal cortex), when they are presented as uninflected stems ('desk, sing'). In contrast, when an inflectional affix is added to the stem (as in 'desks, singing'), then inflected verbs differentially activate left inferior frontal cortex compared with inflected nouns (Tyler et al. 2001, 2004).

The results of both our previous studies therefore suggest that grammatical category per se does not influence the processing of a word when it is encountered as a stem. Nouns and verbs may therefore be represented within an undifferentiated cortical system, which is not divided into different categories or domains (Tyler et al. 2001, 2004). This is not to say that grammatical category information does not constitute part of the lexical representation of the word but rather that category is not a first-order organizing principle of lexical representation in the brain. Encountering a word when the structural implications of the word are relevant, such as when the word is inflected, appears to trigger greater morphological processing for verbs than nouns. This suggests that morphological processing for nouns and verbs may be differently engaged when there is a syntactic context for the word. In summary, this account suggests that noun–verb differences do not reflect differences in their neural representations per se but rather in the differential processing requirements of the 2 types of words due to their differing roles in sentence interpretation.

If, as we propose, inflected verbs result in greater morphological processing due to the assignment of different elements of verb morphology to their appropriate structural roles (e.g., tense or relational roles), we might expect that areas of the language system other than the left inferior frontal gyrus (LIFG) may also be engaged to a greater extent by inflected verbs. We suggest morphological processing may also have implications for activity in regions thought to have a role in lexical processing/representation. As discussed above, grammatical category information may be encoded within the language system at the lexical level. While uninflected noun or verb stems, may readily access lexical representations, the presence of an affix in inflected verbs may place additional demands on this access process. To map onto a lexical representation and interpret an inflected word correctly, the affix needs to be identified and assigned to a specific linguistic function. This further processing may require, in addition to LIFG involvement, the contribution of the left temporal cortex, which may be greater for inflected verbs than inflected nouns due to the additional tense and/or relational roles associated with verbs. Evidence from neuropsychology suggests that left temporal lobe regions—namely middle and superior temporal gyri—play an important role in the mapping of word inputs onto the stored representations of word meaning (Dronkers et al. 2004). Neuroimaging studies have likewise identified these regions as being central to the processing of spoken words (Binder et al. 1996; Indefrey and Levelt 2000; Kaan and Swaab 2002) and sentences (Schlosser et al. 1998). Thus, these regions are plausible candidates for engagement in the additional lexical processing that may be required by inflected verbs. In keeping with these findings, in our own neuroimaging studies we have found that spoken-word processing activates the left middle temporal gyrus (LMTG) (Tyler et al. 2005). Moreover, across a number of studies on morphological processing, the LMTG appears to be coactivated with LIFG when morphologically complex words are processed. For example, in a recent study we reported LMTG and LIFG activation for regularly inflected words ('jumped, played') compared with past tense forms that do not have any overt morphological structure ('slept, taught'; Tyler et al. 2005). Furthermore, a connectivity analysis carried out on these data showed that activation in LIFG predicted activity in the LMTG but only for regularly inflected words (Stamatakis et al. 2005). In addition, LMTG was also activated by inflected verbs in our earlier study (Tyler et al. 2004) but was not reported because it was subthreshold.

We carried out the present study to directly test the hypothesis that nouns and verbs share the same lexical representation and differ in the morphological processes performed upon them, by comparing the neural consequences of processing noun and verb stems and inflected forms. We compared unambiguous noun and verb stems (e.g., 'bullet, sing'), together with their inflectional variants ('bullets, sings'), in an event-related functional magnetic resonance imaging (fMRI) study. In creating inflected forms, we exploited a morphological ambiguity in English, whereby the same affix '-s' is applied to nouns to create plural forms and to verbs to create the third-person singular of the present tense. In this way, factors such as length and orthographic consistency are perfectly matched across inflected nouns and verbs. Subjects were presented with one word at a time and asked to make a timed semantic valence judgment to each word, where they judge each word to be either pleasant or not pleasant. The task involves accessing a word's meaning in order to make the valence decision (Grossman et al. 2002) and should require equivalent processing demands for all words irrespective of grammatical class or form. The task is therefore a suitable probe to directly test predictions, derived from our previous studies (Tyler et al. 2001, 2004), that nouns and verbs are differentiated by virtue of the morphological processes that they invoke rather than by intrinsic differences in their representation. If correct, we should observe no differences in the patterns of activation for noun and verb stems, but inflected verbs should generate increased activation over inflected nouns. Moreover, we predict that this increased activation will be located in the LIFG and LMTG. Even though the task does not require overt morphological manipulation, we still expect morphological processing to occur because many studies have shown that complex words are automatically segmented into their constituent morphemes during processing (Allen and Badecker 1999; Rastle et al. 2000).

Methods

Participants

Twelve healthy right-handed volunteers participated in the study, 9 females and 3 males aged 20–37 years (24.83, standard deviation = ±4.61). Participants were recruited from the Centre for Speech and Language subject pool. Exclusion criteria included history of neurological illness, head injury, or other medical disorder likely to affect cognition. All participants gave informed consent of procedures, and the study received ethical approval from Addenbrookes NHS Trust Ethical Committee.

Materials

The experiment used a 2 × 2 factorial design, with the factors composed of grammatical category (noun or verb) and word form (stem or inflection). Because most words in English are form class ambiguous in that they can function as either nouns or verbs, even if there is a preference for one or other form class, we selected stimuli that met the stringent criterion that nouns did not have a verb frequency and verbs did not have a noun frequency listed in the Celex database (Baayen et al. 1995) (Appendix 1). Nouns and verbs selected in this way were presented either as stems or as regularly inflected forms. We used the same inflection for both grammatical categories—the plural and third-person singular 's' (e.g., 'bullets, sings'). These test items were interspersed with baseline stimuli, which consisted of a series of XXX's, matched in length to stems or inflections. There were 66 items in each condition. Nouns and verbs were matched on imageability, familiarity (both from Medical Research Council (MRC) psycholinguistic database [Coltheart 1981] and pretests carried out in our laboratory), and number of letters (Table 1). A series of *t*-tests investigated differences in familiarity, imageability, and length for nouns and verbs. There was no difference between nouns and verbs in their imageability ($t_{130} = 0.78$; $P > 0.4$, $P > 0.8$), familiarity ($t_{126} = -1.22$, $P > 0.2$), length as stems ($t_{130} = -1.50$, $P > 0.1$), and length as inflected forms ($t_{130} = -1.41$, $P > 0.1$). Finally, items were matched on valence measures. These were obtained from a pretest in which 17 subjects (who did not participate in the imaging study) were presented with each stimulus and asked to decide as quickly as possible whether the word was pleasant or not pleasant. We recorded response latencies as well as subjects' valence decisions. Latencies and preference strength (the difference between the percentage of subjects who judged a stimulus to be pleasant and those who judged it to be unpleasant) did not differ across the 4 conditions (Table 1).

The experiment was divided into 2 sessions with the order of the sessions counterbalanced across subjects. Half of the noun and verb stems appeared in session 1 and half in session 2. Noun and verb stems that appeared in session 1 were presented as inflections in session 2 and vice versa. In this way, all nouns and verbs appeared twice, once as a stem and once as an inflection, thus ensuring that stems and inflected words were perfectly matched on the relevant linguistic variables. To ensure that task difficulty was consistent across the experiment, items in the 2 sessions were matched on familiarity, imageability, number of letters, and valence.

Procedure

We carried out an event-related study that involved presenting written words, one at a time, on a screen via computer using DMDX experimental software (Forster KI and Forster JC 2003). Words were presented for 500 ms with an inter-stimulus interval of 1880 ms in a pseudorandom order, such that there were no more than 4 consecutive items from each condition and ensuring that all conditions appeared equally often before and after baseline items. We did this as a precaution against extraneous task-switching effects appearing disproportionately in one condition. Subjects' performed a valence judgment (pleasant/not pleasant) on each word and indicated their judgment by pressing 1 of 2 response buttons. Subjects did not respond to baseline items. The baseline items consisted of a series of XXX's, matched in length to stems or inflected words. A fixation cross appeared at the beginning of the experiment for 30 s and also at the end. Subjects were instructed to focus on this cross.

Table 1
Item statistics

		Familiarity[a, b]	Imageability[a, b]	Length	Valence[a] RT (ms)	Valence[a] Preference strength (%)
Nouns	Stem	472 (78)	461 (104)	4.9 (1.1)	700	70
	Inflected form	As above	As above	5.9 (1.1)	691	71
Verbs	Stem	495 (73)	447 (93)	5.2 (1.5)	702	68
	Inflected form	As above	As above	6.3 (1.5)	685	72

[a]Pretests conducted in our laboratory.
[b]Data from MRC Psycholinguistic Database (Coltheart 1981).

Image Acquisition and Analysis

The fMRI was performed on a 3-T Bruker Medspec Avance S300 system, using a gradient-echo echo planar imaging sequence (time repetition = 1.1 s, echo time = 27.5 ms, flip angle = 65°, field of view = 20 × 20 cm) with head coils, 143-kHz bandwidth, and spin-echo–guided reconstruction. Altogether 996 volumes were collected over 2 sessions, consisting of 21 oblique slices, 4-mm thick (1-mm gap between slices, 3.1 × 3.1 mm in-plane resolution) from each subject. T_1-weighted scans were acquired for anatomical localization. Data were analyzed using Statistical Parametric Mapping (SPM99) (Friston et al. 1995), implemented in MATLAB version 5.2 (The Mathworks Inc., Natick, MA).

Prior to model application, brain volumes from each subject were corrected for slice time acquisition and realigned to the first volume. Functional images were then spatially normalized into the standard stereotactic space of Talairach and Tournoux (1988), using a set of 12 parameter linear affine transformations and 7 × 8 × 7 nonlinear basis functions. Because our previous research showed that the loss of blood oxygenated level-dependent signal near air-tissue interfaces at high magnetic field strengths (Devlin et al. 2000) may lead to errors in normalization, we masked areas of susceptibility prior to normalization. Masking was done by hand using MRIcro (Chris Rorden, chris.rorden@nottingham.ac.uk), and areas affected by susceptibility in each affected slice were filled. This mask was saved as a region of interest and then used during normalization (the masked areas were then not taken into account during normalization).

Following this, we applied spatial smoothing with an isotropic Gaussian kernel filter of 10 mm to account for small-scale variations in individuals' sulcal and gyral anatomy and to render the data more normally distributed (by the central limit theorem). Data were analyzed with a random effects model. For every subject, a single mean contrast image was produced for each comparison. The set of voxel values for each contrast constituted a statistical parametric map of the *t* statistic, SPM (*t*), which was then transformed to the unit normal distribution, SPM (*Z*). We thresholded the activations at a voxel threshold of 0.001 uncorrected and accepted as significant those clusters that survived at $P < 0.05$ corrected for multiple comparisons for the entire brain. Because our main focus is on prespecified regions within the neural language system—the inferior frontal cortex and middle temporal gyrus—for these regions, we report activations that survive an uncorrected threshold of $P < 0.001$ but which are significant at $P < 0.05$ when a small volume correction (SVC) (based on a sphere of diameter 10 mm, centered on the peak coordinates as identified by voxel-level thresholding for each contrast of interest) (Worsley et al. 1996) is applied. As SPM coordinates are given in Montreal Neurological Institute space, regions were identified by converting the coordinates to Talairach space with a nonlinear transform (Brett et al. 2001).

Results

Behavioral Results

For each stimulus, we calculated the mean percentage pleasantness strength. An analysis of variance (ANOVA) with one repeated measure (word form: stem or inflected form) and one independent measure (grammatical category: noun or verb) showed that for both word form and grammatical category, there were no differences in any of the valence judgment measures and no interactions (all Fs < 1). Response latencies were also collected on all items. Each data point was inverse transformed to correct for outliers (Ulrich and Miller 1994), and means for each condition were calculated (see Fig. 1). The data were analyzed in a 2 × 2 ANOVA with 2 repeated measures (word form: stem or inflected word and grammatical category: noun or verb) in the subjects' analysis ($F1$) and one repeated measure (word form) and one between items measure (grammatical category) in the items analysis ($F2$). Latencies to inflected words were slightly slower (888 ms) than to stems (867 ms) ($F1_{1,11} = 4.06$, $P < 0.07$; $F2_{1,130} = 5.33$, $P < 0.025$), presumably due to the fact that inflected words were longer than stems by one letter. There were no differences in latencies as a function of grammatical category ($F1_{1,11} = 2.57$, $P > 0.1$; $F2 < 1$) and no interaction between category and word form (both Fs < 1; see Fig. 1).

Imaging Results

Comparing all words against the baseline (Table 2, C), we found significant clusters of activation in the bilateral cerebellum, associated with the button-pressing task, which was not involved in the baseline condition. We also found significant activation in the left fusiform (Brodmann area [BA] 37) close to the region implicated in visual word form processing (Cohen and Dehaene 2004), left postcentral gyrus (BA 1 and 2) extending to the left inferior parietal cortex (BA 40), in addition to activation in the LIFG extending from BA 44 to 45, a cluster in left supplementary motor area (BA 6) and one in left putamen which extended laterally into the insula. These regions are typically activated in language processing tasks involving written words (e.g., Vandenberghe et al. 1996; Polk and Farah 2002; Cohen and Dehaene 2004).

Stems and inflected words activated essentially the same primarily left-lateralized neural network, with greater activation for inflected words compared with stems especially in left frontal cortex (Fig. 2*A*,*B*). Comparing stems against baseline (Table 2, A; Fig. 2*A*) produced activations in bilateral cerebellum, left postcentral gyrus (BA 2) extending to inferior parietal cortex (BA 40), and the LIFG (BA 44 and 45). Moreover, there were no areas of the left-lateralized language system that were activated more strongly for either noun stems or verb stems, even when we lowered the threshold to $P < 0.01$. Compared with baseline, inflected words (Table 2, B; Fig. 2*B*) activated a similar network as the stems: bilateral cerebellum, fusiform (BA 37), left postcentral gyrus (BA 1/2) extending to left inferior parietal cortex (BA 40), and also LIFG. While the LIFG activation for stems included BA 44 and 45, a more extensive left frontal region was activated for inflected words that extended from BA 45 to 44 and included the precentral gyrus (BA 6). A second more anterior LIFG cluster was also activated, extending from BA 45 to 47.

This greater LIFG activation for inflected words showed up the direct contrast between inflected words compared with stems (Table 3, A), where 2 LIFG regions were significantly more active for inflected words—one of 106 voxels in BA 44 and a smaller cluster in BA 47 (peak: –24, 35, –8) (with SVC) and another lying in the posterior portion of the LMTG (BA 21) (34 voxels at –63, –39, 4) (with SVC). This increased activation for inflected words is shown in Figure 3 where we plot at the peak voxels of the 2 LIFG clusters and the LMTG cluster. The individual contrast of inflected verbs compared with verb stems (Table 3, B) showed significantly greater LIFG activation (with SVC) and also greater LMTG activation, although this second cluster was only significant at a lower threshold of $P < 0.01$ uncorrected. The contrast of inflected nouns against noun stems also showed greater LMTG activation at a lower threshold of $P < 0.01$ uncorrected (Table 3, C). When we directly compared inflected verbs with inflected nouns, the very posterior portion of the LMTG was more strongly activated (with SVC) for inflected verbs (–51, –42, 9) (Table 3, D). The reverse contrast of inflected nouns compared with inflected verbs did not reveal any significant activations.

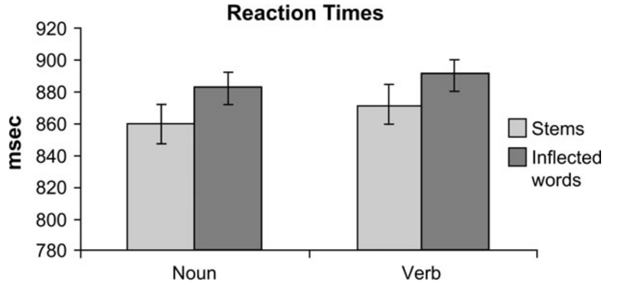

Figure 1. Retransformed valence judgment latencies (ms) and standard errors for the 4 experimental conditions.

Table 2
Brain areas activated in the contrast of (A) both stems versus baseline, (B) both inflections versus baseline, and (C) all words minus baseline

Brain region	BA	Cluster level *P*-corrected	Extent	Voxel level *P*-corrected	Coordinates *x, y, z*	*Z* value
(A) Both stems versus baseline						
L postcentral gyrus	**2**	**0.000**	**431**	**0.148**	**−40, −24, 42**	**4.66**
	2			0.777	−56, −22, 37	3.94
LIFG	**44**	**0.021**	**168**	**0.890**	**−57, 13, 16**	**3.80**
	45			0.996	−44, 22, 28	3.43
R cerebellum		**0.000**	**508**	**0.142**	**6, −63, −15**	**4.67**
				0.511	20, −56, −28	4.19
L cerebellum		**0.010**	**104**	**0.827**	**−34, −46, −23**	**3.88**
				0.999	−42, −49, −18	3.34
(B) Both inflections versus baseline						
L fusiform	**37**	**0.000**	**726**	**0.320**	**−42, −47, −16**	**4.51**
L cerebellum				0.436	−44, −63, −19	4.39
L postcentral gyrus	**1**	**0.000**	**807**	**0.051**	**−55, −19, 38**	**5.08**
	1/2				−38, −23, 42	4.53
L inferior parietal lobe	40				−48, −33, 46	4.33
LIFG	**45**	**0.000**	**826**	**0.410**	**−48, 24, 17**	**4.41**
	44				−40, 7, 25	4.36
L precentral gyrus	6				−48, 11, 12	4.28
LIFG	**45**	**0.000**	**826**	**0.410**	**−50, 27, 4**	**4.41**
	47				−36, 33, 0	4.17
	47				−32, 30, −12	3.64
R cerebellum		**0.000**	**1574**	**0.097**	**4, −49, −6**	**4.90**
L cerebellum				0.215	6, −71, −20	4.65
R cerebellum				0.217	16, −55, −16	4.64
(C) All words versus baseline						
L postcentral gyrus	**1**	**0.000**	**724**	**0.044**	**−55, −19, 38**	**5.05**
	2				−40, −23, 42	4.78
	1				−46, −25, 47	4.31
R cerebellum		**0.000**	**1164**	**0.141**	**4, −49, −4**	**4.71**
L fusiform	**37**	**0.000**	**635**	**0.478**	**−42, −49, −18**	**4.26**
L cerebellum				0.633	−34, −46, −23	4.12
L fusiform	37			0.701	−46, −61, −17	4.05
L medial frontal gyrus	**6**	**0.019**	**157**	**0.526**	**−4, 12, 56**	**4.22**
LIFG	**44**	**0.052**	**121**	**0.653**	**−40, 9, 27**	**4.10**
L putamen		**0.033**		**0.791**	**−28, –12 −4**	**3.96**
LIFG	**44**	**0.001**	**304**	**0.823**	**−48, 12, 12**	**3.93**
LIFG	45			0.840	−50, 22, 19	3.91
LIFG	44			0.906	−57, 12, 16	3.81

Note: We report clusters significant at $P < 0.05$ after statistical correction. Cluster maxima are highlighted in bold. Multiple peaks within an extent are shown on subsequent lines. Coordinates are presented in Talairach space. L, left; R, right.

Given the issues that prompted this study, the most important analysis is the interaction between grammatical category (noun/verb) and word form (stem/inflected form). Based on our previous studies, we predicted that inflected verbs compared with their stems should more strongly activate LIFG and LMTG than inflected nouns compared with their stems. This interaction produced significant activation (with SVC) both in LIFG (–22, 22, –14) and in LMTG (–46, –24, –14) (Table 4). The results of the simple main effects and the plots shown in Figure 4 suggest that the interaction was driven by increased LIFG activation to inflected verbs relative to verb stems. There was no evidence of LIFG or LMTG activation to inflected nouns compared with noun stems even when we reduced the threshold. This frontal and temporal activation overlaps with the activation we found in 2 previous studies examining the neural processing of inflected words (see Discussion).

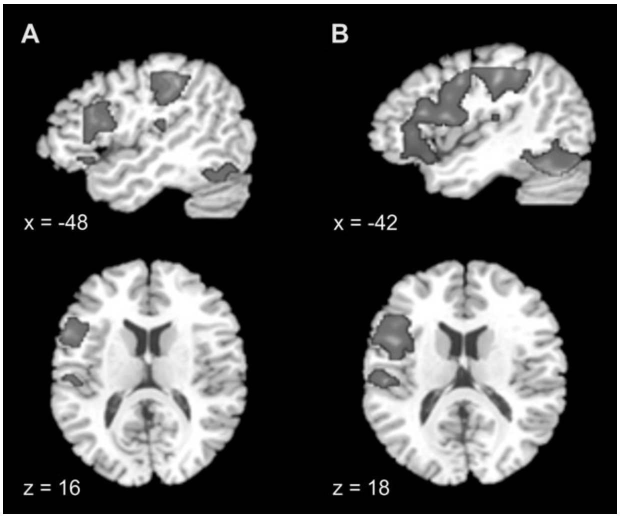

Figure 2. (*A*) Stems versus baseline, (*B*) inflected words versus baseline significant activations thresholded at $P < 0.01$ uncorrected, overlaid on sagittal and axial slices of a canonical high-resolution structural image in Montreal Neurological Institute space (MRIcro software, www. psychology.nottingham. ac.uk/staff/cr1/mricro.html).

Discussion

In the current study, healthy volunteers were presented with unambiguous nouns and verbs as stems or inflected forms. As hypothesized on the basis of our previous research (Tyler et al. 2001), we found that when words are encountered as stems, nouns and verbs activate a similar widespread left-hemisphere network, including fusiform (BA 37), postcentral gyrus (BA 1 and 2), inferior parietal cortex (BA 40), and IFG (BA 44 and 47), areas which are typically associated with processing written words (e.g., Vandenberghe et al. 1996). Moreover, this lack of differentiation cannot be accounted for by the ubiquitous form—class ambiguity which is found in English because the words were unambiguously either nouns or verbs. Nor can they be attributed to differences in the difficulty with which nouns and verbs were processed in this task because there were no behavioral differences in reaction times.

However, consistent with our previous study of verb and noun inflection (Tyler et al. 2004), differentiation did clearly emerge when a grammatical morpheme was added (realized as '-s' in the case of both nouns and verbs) to stems to produce

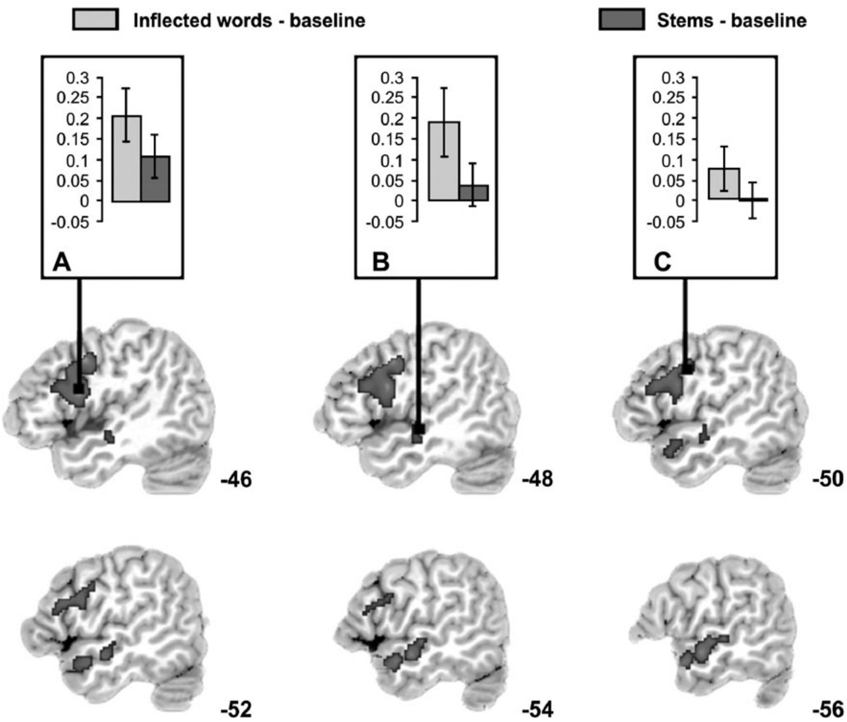

Figure 3. Series of sagittal slices displaying the greater activation for inflected words over stems. Activations were overlaid on a canonical high-resolution structural image in Montreal Neurological Institute space (MRIcro software, www. psychology.nottingham. ac.uk/staff/cr1/mricro.html). Greater LIFG (BA 44/45/47) and MTG activation for inflected words are shown. The plots show the effect size at statistical peak voxel in each cluster for the contrasts of inflected words over baseline and stems over baseline in (*A*) LIFG BA 44/45 at −38, 16, 14; (*B*) MTG (BA 21) at −63, −39, 4; and (*C*) LIFG BA 47 at −24, 35, −8.

a morphologically complex word. In this case, we found greater LIFG and LMTG activation for inflected words compared with stems, which was stronger for inflected verbs compared with inflected nouns. This result is partially consistent with Perani's (Perani et al. 1999) findings of differential patterns of activation for nouns and verbs. In that study, the words were all inflected (because they were Italian and all Italian words are inflected) and differences in neural activation were seen in areas that included the left frontal cortex (BA 45, 46, 9), as well as superior parietal (BA 7), anterior temporal (BA 22/38), middle temporal (BA 21/37), and occipital (BA 18) regions.

Our results are largely incompatible with the claim that nouns and verbs are represented and/or processed in distinct neural regions on the basis of grammatical category per se. For this to be the case, noun and verb stems should have activated distinct neural regions in this study, which they did not. Similarly these results rule out a neural organization of nouns and verbs based on their differing semantic properties (Gentner 1981; Bock and Miller 1991) because this would also predict differences in activation for noun and verbs stems. Instead, these findings reinforce our earlier claim that nouns and verbs are represented and processed within the same distributed neural language system, which is modulated as a function of the processing that different types of linguistic inputs entail. This may help to explain why lesion-behavior associations rarely produce a consistent relationship between lesion location and behavioral deficits for either nouns or verbs.

One potential limitation of the current study is that our stimuli were presented only as single items, whereas many cases of verb/noun dissociation within the neuropsychological literature tend to occur when verbs and nouns are presented in some form of context such as a phrase or sentence (e.g., McCarthy and Warrington 1985; Daniele et al. 1994). Because a major function of morphological affixes is to play a relational role in sentences, it could be argued that we have underestimated the potential effects of morphology by using single words. Although possible, we think this is unlikely in the light of recent results from our laboratory. In an fMRI study, subjects read uninflected nouns and verbs when they occurred either in isolation or in phrasal contexts. Consistent with the findings of the present study, uninflected nouns and verbs activated

Table 3

Brain areas activated in the contrast of (A) both inflected forms minus both stems, (B) inflected verbs minus verb stems, (C) inflected nouns minus noun stems, and (D) inflected verbs minus inflected nouns

Brain region	BA	Cluster level *P*-corrected	Extent	Voxel level *P*-corrected	Coordinates *x, y, z*	*Z* value
(A) Inflected words versus stems						
LIFG	**44/45**	**0.010**	**106**	**0.630**	**−38, 16, 14**	**4.33**
LIFG	44			0.721	−44, 7, 18	4.25
LIFG	**47**	**0.026**	**6**	**0.044***	**−24, 35, −8**	**3.57**
LMTG	**21**	**0.011**	**34**	**0.024***	**−63, −39, 4**	**3.84**
(B) Inflected verbs versus verb stem						
LIFG	**47**	**0.036**	**8**	**0.045***	**−22, 19, −14**	**3.45**
LMTG**	**21**	**1.00**	**1**	**1.00**	**−59, −22, −3**	**3.11**
(C) Inflected nouns versus noun stems						
L precuneus	**7**	**0.003**	**173**	**0.086**	**−16, −66, 36**	**4.96**
	31			1.00	−14, −66, 25	3.42
L Cuneus	19			1.00	−26, −58, 34	3.40
LMTG**	**21**	**1.00**	**1**	**1.00**	**−49, −60, 5**	**3.29**
(D) Inflected verbs versus inflected nouns						
LIFG	**44**	**0.042**	**3**	**0.051***	**−40, 8, 12**	**3.35**
LMTG	**21**	**0.033**	**15**	**0.019***	**−51, −42, 9**	**4.11**

Note: Clusters significant at $P < 0.05$ after statistical correction are reported. Cluster maxima are highlighted in bold. Multiple peaks within an extent are shown on subsequent lines. Coordinates are presented in Talairach space. L, left; R, right. *Significant corrected P values shown after SVC (sphere of 10 mm radius, centered on the peak voxel). **Clusters significant at a height threshold of $P < 0.01$.

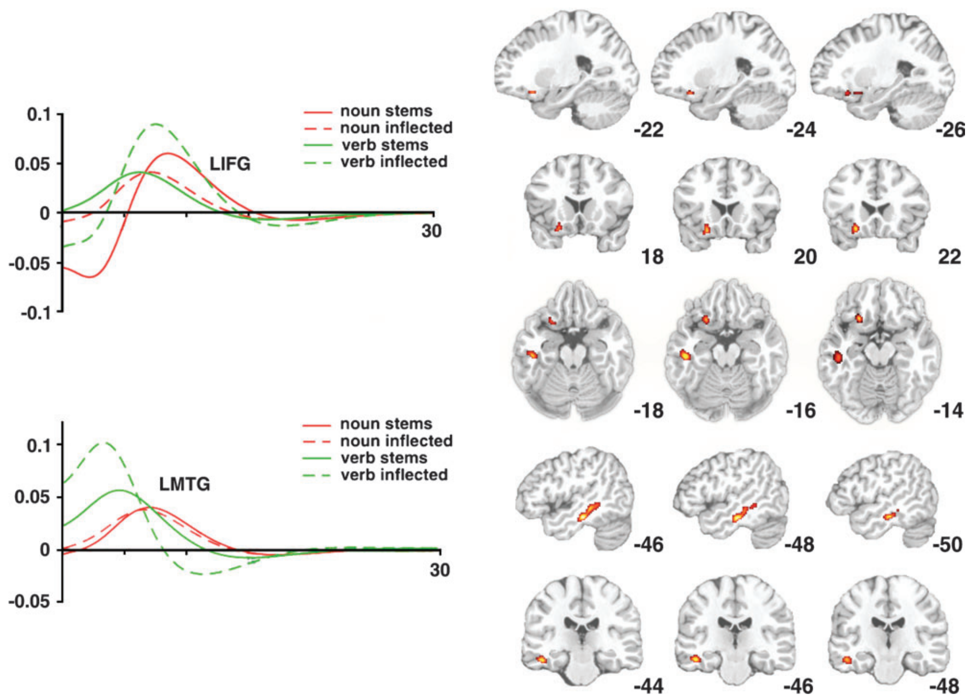

Figure 4. Interaction of grammatical category by word form (inflected verbs vs. verb stems relative to inflected nouns vs. noun stems). A series of axial, coronal, and sagittal slices shows the location of the significant clusters. Activations were overlaid on a canonical high-resolution structural image in Montreal Neurological Institute space (MRIcro software, www. psychology.nottingham. ac.uk/staff/cr1/mricro.html). Left is Left. The peristimulus time plots show response according to stimulus type (inflected nouns, noun stems, inflected verbs, and verb stems) at the peak voxel of LIFG activation −22, 22, −14 (top) and the peak voxel of left MTG activation –46, −22, −16 (bottom plot).

Table 4
Brain areas activated for the interaction contrast between word form and grammatical class (inflected verbs vs. verb stems compared with inflected nouns vs. noun stems)

Brain region	BA	Cluster level *P*-corrected	Extent	Voxel level *P*-corrected	Coordinates *x, y, z*	*Z* value
LMTG	**21**	**0.016**	**10**	**0.030***	**−46, −24, −14**	**3.57**
LIFG	**47**	**0.035**	**4**	**0.052***	**−22, 22, −14**	**3.35**

Note: Clusters significant at $P < 0.05$ after statistical correction are reported. Cluster maxima are highlighted in bold. Coordinates are presented in Talairach space. L, left; R, right. *Significant corrected *P* values shown after SVC (sphere of 10 mm radius, centered on the peak coordinate).

essentially the same neural system. In addition, verbs generated additional LMTG activity compared with nouns, but only when they occurred in a phrasal context, as we discuss in detail below (Kherif et al. 2005).

The addition of an inflectional morpheme to stems to produce a complex word in English strongly highlights aspects of its grammatical function. For the system to gain access to this structural information, a word first needs to be decomposed into its stem and affix. At this stage, the word's form class becomes relevant for the interpretation of the affix. Unless the stem is classified as either a noun or a verb, the status of the affix remains unclear—the affix /-s/, for example, either can be a plural marker or can mark the third-person singular. It is only when the form class of the stem is identified that the function of the affix can be disambiguated. The resulting combination of stem and affix enables the appropriate structural implications of a complex word to be activated. The results described here suggest that it is only after a complex word has been decomposed into its component morphemes that its form class has processing consequences. This in turn produces differential activation within the neural language system. On this account, grammatical category information is encoded within the language system at the lexical level. Accessing this information, however, does not inevitably give rise to differential activations for nouns and verbs; it only does so when there are structural implications to grammatical category knowledge. In the present study, we see this in the stronger left frontotemporal activation for inflected verbs, which carry tense and play a relational role in the interpretation of sentences by specifying the relations between the elements of a phrase or sentence (e.g., Gentner 1981). Nouns on the other hand refer to object-like elements (people, places things) within a sentence, and noun inflection tends to have a more semantic role, for example number (Gentner 1981; Langacker 1987). Word class effects therefore appear to be associated with the roles that lexical items play within structural contexts such as a sentence or phrase. Moreover, this account predicts a similar increase in left frontotemporal activation when verb stems occur in structural contexts other than complex words, such as in short phrases ('they eat'). This is indeed the result we have obtained in a recent fMRI study in which subjects saw written word class ambiguous words which appeared either as single words (e.g., 'lock') or within a phrase disambiguated as a noun (e.g., 'the lock') or as a verb (e.g., 'to lock'). Consistent with the present results, single homophones, whether they were more likely to be interpreted as a noun (e.g., 'farm') or a verb (e.g., 'lift'), activated the same left frontotemporal system. However, when the same homophones occurred in a phrase as a verb, they generated stronger activation within LMTG than did homophones in phrases disambiguated as nouns (Kherif et al. 2005).

The LIFG and LMTG regions that were activated for inflected words are not uniquely involved in morphological and grammatical processing, although a growing body of research suggests that these regions are more strongly engaged by such processes. For example, we have previously reported LMTG and LIFG activation for regular ('jumped, played') compared with irregular past tense forms, which do not have an overt morphological structure ('slept, taught'; Tyler et al. 2005). A connectivity analysis carried out on these data indicated that LIFG activation predicted activity in the LMTG more strongly for regularly compared with irregularly inflected words suggesting that frontal and temporal regions are part of an integrated system modulated by morphological regularity (Stamatakis et al. 2005). Other functional imaging studies also suggest an interaction between these regions in the processing of linguistic structure. For example, Rodd et al. (2005) report coactivation of LIFG and LMTG in syntactic processing. Similarly, Keller et al. (2001) found syntactic processing and maintenance required coordinated communication between LIFG areas and left middle and superior temporal gyrus.

Finally, it should be pointed out that some researchers have argued that only tasks that explicitly tap into grammatical knowledge can effectively examine differences between various grammatical categories such as nouns and verbs (Shapiro et al. 2005, Shapiro and Caramazza 2003). This assumes that grammatical category information can only be accessed under specific conditions and rules out the possibility that this type of information can be automatically accessed as part of each lexical representation. Our results would suggest that this is not the case. In the current study, in order to determine whether grammatical category information is automatically activated when unambiguous nouns and verbs are encountered, subjects were required to make a valence judgment to each word presented. This task does not require explicit access to grammatical category information, and we found evidence for differences between the processing of inflected nouns and verbs, suggesting that grammatical category information can be accessed during an implicit task. In addition, in our previous study (Tyler et al. 2004), we used a semantic categorization task to examine differences between inflected nouns and verbs. This task was also an implicit test of inflectional processing and showed that differences in grammatical processing can be examined without requiring subjects to overtly manipulate grammatical information.

In summary, our findings speak directly to the controversy of whether grammatical categories are represented in distinct neural substrates and provide strong evidence that nouns and verbs do not show differential activation when presented as uninflected stems but differ in the neural processes that operate over morphologically complex forms. We thus argue that there is no compelling evidence to suggest that grammatical category acts as a first-order organizing principle underlying the neural representation of words but rather that it interacts with processes that operate over lexical representations. Our findings demonstrate that the frontotemporal neural system involved in language processing is strongly involved in the processing of inflected words with inflected verbs placing greater demands on this system than inflected nouns, perhaps due to the additional structural implications of verbs with regards to sentence interpretation.

Notes

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Appendix 1 Experimental items

Unambiguous nouns

affair	bean	belief	blade	bullet	camel
canal	cereal	chore	clan	corpse	costume
crime	deceit	dogma	ego	event	fact
farce	flea	fraud	frock	germ	goat
grove	horror	jay	joy	lantern	loss
mite	mood	myth	nephew	noise	ode
planet	plea	porch	problem	realm	reed
rite	role	rug	shark	snail	spasm
speech	pider	success	sword	talent	tariff
theft	thorn	threat	tomb	urn	vale
vase	verb	victim	wagon	weapon	woe

Unambiguous verbs

admit	allow	applaud	argue	arrive	assist
avoid	awaken	bake	beg	breathe	bury
carve	cling	conceal	conquer	die	dine
disappear	drown	earn	eat	fade	fail
follow	forget	frighten	greet	heal	hear
hover	ignore	juggle	mar	marry	mow
pour	pray	prevent	prosper	pursue	refuse
retain	roam	rob	seek	seize	send
sever	sew	shatter	shrivel	shut	sing
sit	soothe	speak	spend	straighten	strangle
succeed	suffer	tempt	tire	unlock	vanish

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