

Cortical Differentiation for Nouns and Verbs Depends on Grammatical Markers

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Abstract

■ Here we address the contentious issue of how nouns and verbs are represented in the brain. The co-occurrence of noun and verb deficits with damage to different neural regions has led to the view that they are differentially represented in the brain. Recent neuroimaging evidence and inconsistent lesion–behavior associations challenge this view. We have suggested that nouns and verbs are not differentially represented in the brain, but that different patterns of neural activity are triggered by the different linguistic functions carried by nouns and verbs. We test these claims in a functional magnetic resonance imaging study using homophones—words which function grammatically as nouns or verbs but have the same form and meaning—ensuring that any neural differences reflect differences in grammatical function. Words were presented as single

stems and in phrases in which each homophone was preceded by an article to create a noun phrase (NP) or a pronoun to create a verb phrase (VP), thus establishing the word's functional linguistic role. Activity for single-word homophones was not modulated by their frequency of usage as a noun or verb. In contrast, homophones marked as verbs by appearing in VPs elicited greater activity in the left posterior middle temporal gyrus (LpMTG) compared to homophones marked as nouns by occurring in NPs. Neuropsychological patients with grammatical deficits had lesions which overlapped with the greater LpMTG activity found for VPs. These results suggest that nouns and verbs do not invariably activate different neural regions; rather, differential cortical activity depends on the extent to which their different grammatical functions are engaged. ■

INTRODUCTION

The distinction between nouns and verbs is almost universal across the world's languages (Robins, 1952). Nouns refer to concrete entities (*ball, photograph*) and abstract concepts (*hope, trust*) and tend to function as agents, instruments, or recipients, whereas verbs denote actions, states, and events. Perhaps the clearest functional distinction between these two classes of words is that verbs are primarily relational; they relate subjects and objects, agents and recipients (Bock & Miller, 1991; Langacker, 1987; Gentner, 1981). Verbs, therefore, serve a key grammatical function in sentences, binding the structural elements and meanings denoted by words into a coherent representation.

Given their complementary linguistic functions, it is not surprising that nouns and verbs have long been claimed to have distinct neural representations, reflecting modular principles that govern the representation of linguistic knowledge in the brain. The evidence for the claim for separable neural systems for nouns and verbs primarily comes from neuropsychological data in which some patients appear to have a deficit for verb processing with spared noun processing (Breedin, Saffran, & Schwartz, 1998; Rapp & Caramazza, 1997; McCarthy &

Warrington, 1985), whereas others show the reverse pattern of having more difficulty with nouns (Damasio & Tranel, 1993; Zingeser & Berndt, 1990). As patients with verb deficits sometimes have damage to the left frontal cortex, and patients with noun deficits sometimes have damage to the left temporal lobe (Damasio & Tranel, 1993), these associations are taken as support for the hypothesis that nouns and verbs are processed in neurally distinct regions (Shapiro, Moo, & Caramazza, 2006). However, there are several reported exceptions to this pattern (Silveri & Di Betta, 1997; De Renzi & Pellegrino, 1995) and these kinds of dissociations in and of themselves do not clarify the cognitive basis of noun–verb deficits which can be due to lexical, morphological, semantic, or syntactic differences (Caramazza & Mahon, 2003). Moreover, naturally occurring lesions are rarely confined to discrete regions, and therefore, it is difficult to draw inferences about the neural bases of cognitive functions purely on the basis of lesion–behavior associations.

Because of these limitations, the hypothesis that there are neural distinctions on the basis of grammatical category has also been investigated in neuroimaging studies with healthy participants. Once again, the picture is somewhat mixed. Some studies have reported greater activity in the left inferior frontal cortex for processing verbs compared to nouns (Palti, Shachar,

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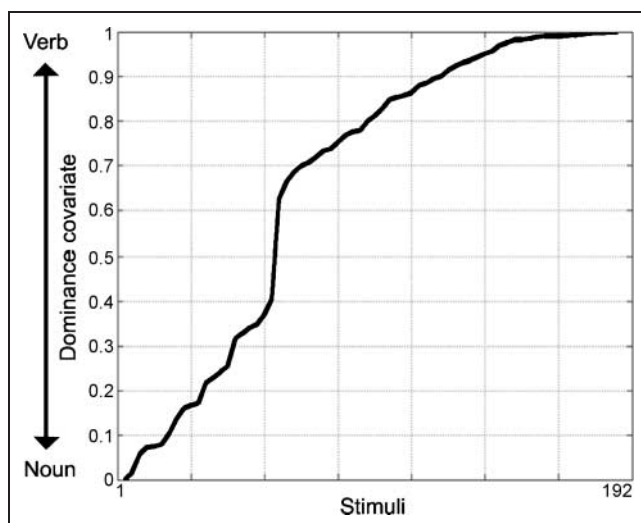


Figure 1. Dominance distribution of the 96 stems in this experiment. Stems ranged in frequency of use from almost noun-exclusive (0) to verb-exclusive (1). For each homophone, we used the formula $[\delta = \tan^{-1} [fV/fN]]$ to compute dominance (δ) as a function of the relationship between the frequency as a verb (fV) and frequency as a noun (fN).

nouns and verbs are associated with different neural regions, each category of stimulus should always activate the same distinct regions. This would predict that homophones which are used most frequently as verbs should always activate those regions associated with verb processing (e.g., frontal cortex) whether they are presented as stems or within VPs, whereas homophones which are used most often as nouns should always activate those neural regions associated with noun processing (e.g., temporal cortex), irrespective of their context. In the scanner, subjects made a valence judgment (pleasant/unpleasant judgment) to each stimulus by means of a button-press response (Grossman et al., 2002). We chose this task because it is unrelated to the nature of the stimuli (i.e., to their grammatical category), and therefore, avoids metalinguistic effects and should tap into more automatic aspects of language processing. Subjects also saw a series of xx (xxxx, xx xxxx) matched in length to each stimulus which constituted the base-line condition.

METHODS

Participants

Fifteen right-handed participants, aged between 19 and 47 years (10 women, 5 men), were recruited from the University of Cambridge staff and student population. Exclusion criteria included history of neurological illness, head injury, or other medical disorder likely to affect cognition. All gave informed consent and were paid for their participation. The study received ethical approval from Addenbrooke's NHS Trust Ethical Committee.

Materials and Procedure

The stimuli consisted of 192 words that were ambiguous between nouns and verbs. These words were presented both as stems (e.g., *smell, cough*) and disambiguated in short phrases (e.g., *a smell, I cough*) in which each stem was preceded by a closed-class item (the, to, etc). The length of the closed-class items was matched in both types of phrases (Table 1b). We refer to these as NPs and VPs for ease of explanation, although the VPs are not VPs in the formal linguistic sense (Crystal, 1980). There were 96 NPs and 96 VPs. Each word appeared once as a stem and once as either an NP or a VP.

Because the words varied in their frequency of use as either a noun or a verb, we avoided binarizing the noun–verb distinction and instead adopted a more sensitive measure of the relative frequency of a word's use as

Table 1. Details of the Experimental Stimuli

(a) Mean Descriptive Statistics for Stems Divided for Presentation as Noun Phrases and Verb Phrases

	Word Form Frequency ^a		Dominance ^b	Letters	Fam ^c	Imag ^c
	Noun	Verb				
<i>Noun Phrase</i>						
Mean	20	15	0.56	4.8	523	467
SD	33	29	0.41	1.1	65	94
<i>Verb Phrase</i>						
Mean	19	16	0.54	4.7	506	465
SD	23	31	0.42	1.1	68	91

(b) Examples of Stimuli

Stem	Phrase
<i>Noun More Frequent</i>	
battle	a battle
chat	I chat
<i>Verb More Frequent</i>	
burn	the burn
drive	you drive
<i>Noun = Verb</i>	
shout	this shout
visit	they visit

^aCombined written and spoken word form frequency per million in the CELEX Lexical Database (Baayen, Pipenbrook, & Gulikers, 1995).

^bDominance refers to the relative frequency as nouns or verbs of the subset of stems that became noun phrases or verb phrases.

^cRatings taken from the MRC Psycholinguistic Database (Coltheart, 1981) and from pretests conducted at CSL.

either a noun or a verb and included this as a parametric modulator in the imaging analysis. A categorical design, where stems were simply modeled in two subgroups (nouns, verbs) based on frequency information, would have been inadequate because it would have ignored the continuous nature of dominance. For each word, we calculated its noun–verb dominance (i.e., its relative frequency as a noun or a verb). Dominance was calculated using the formula in Figure 1, which gave a value between 0 (*very noun dominant*) and 1 (*very verb dominant*). A negative correlation for the modulator would indicate that activity increases with the increasing frequency of a word’s usage as a noun (increasing “nouniness”), showing greater activation for values closer to 0. A positive correlation, showing more activation for values closer to 1, would indicate increasing activity as a word is more frequently used as a verb (increasing “verbiness”). We ensured that there was a fairly even spread of words across the range from 0 to 1. Because stems were invariably shorter than phrases, we also included number of letters in each stimulus as a second parametric modulator. The four sets of stimuli were matched on imageability, frequency, and familiarity (see Table 1a). Examples of the stimuli in each condition are given in Table 1b. We also included a baseline condition to control for low-level visual processing. Each baseline item was a series of *x*s. There were 64 items matched to each of the stems (e.g., xxx or xxxxxx) and 64 matched to each of the phrases (e.g., xxx xxxx or xxxxxx). No response was required for the baseline items.

Each stem or phrase was presented on a screen that was projected via a mirror to participants in the scanner. All words were presented at a comfortable viewing size as determined in a behavioral pilot study. Stimuli were presented for 500 msec, with an intertrial interval of 1880 msec. Participants decided whether the word or phrase was pleasant or not pleasant (Grossman et al., 2002), and pressed the appropriate button on a response box to indicate their choice. We chose this valence task as it was orthogonal to the form-class variable, which was the factor of interest in this study. Pretests carried out in our laboratory on 16 participants who did not take part in the fMRI study showed that NPs and VPs were matched on their valence (i.e., there was no difference in the percentage of pleasant or not pleasant judgments). Moreover, there was a high degree of consistency in the pleasantness ratings given to each homophone when it occurred as a stem or in a phrase ($r = .926$), reflecting the fact that we had selected homophones which had the same meaning as both a noun and a verb. Stems, phrases, and baseline items were pseudorandomly ordered and presented in two blocks of trials, the order of which varied across participants with 96 stems—48 NPs and 48 VPs in each session. Presentation was controlled so that half of the items appeared as stems first and half as phrase first. In

two counterbalanced blocks, participants were asked to decide whether each word or phrase was pleasant or not pleasant as quickly and accurately as possible by pressing the appropriate response button. During the baseline trials, participants were asked to refrain from responding. Reaction time data were collected during the scanning experiment.

Scanning was carried out on a 3-T Bruker Medspec Avance S300 system at the Wolfson Brain Imaging Centre, Cambridge, England. A gradient-echo, echo-planar imaging (EPI) sequence was used (TR = 1.1 sec; TE = 27.5 msec; flip angle = 65°, FOV = 20 × 20 cm, 21 oblique slices, 4 mm thick), 1 mm gap between slices, 128 × 128 in-plane resolution, 1222 repetitions with head coils, 143 kHz bandwidth and spin-echo-guided reconstruction. T1-weighted scans were acquired for anatomical localization.

fMRI Data Analysis

Data analysis was performed using SPM5 software (Wellcome Institute of Cognitive Neurology, www.fil.ion.ucl.ac.uk) implemented in Matlab (Mathworks, Sherborn, MA). Preprocessing of the data involved image realignment and slice timing correction, followed by spatial normalization to a standard EPI MNI template and spatial smoothing with an isotropic 8-mm Gaussian kernel. A temporal high-pass filter (128-sec cutoff) was also applied to remove low-frequency components in the time series. The data for each subject were modeled using the general linear model (Friston et al., 1995). Two sessions, five variables (stem, NP, VPs, baseline for stems, and baseline for phrases) and two parametric modulators (dominance and number of letters in the stimulus) were modeled using the canonical hemodynamic response function with temporal derivatives. We used length-matched baselines for stems and phrases to factor out effects of differences in length between the two. Contrast images from each subject were combined into a group random effects analysis. Results were thresholded at voxel-level threshold of $p < .001$, uncorrected with a random field corrected p value of $p < .05$ for clusters adjusted for the entire brain, unless otherwise stated. SPM coordinates are given in MNI space. To identify regions, these were converted into Talairach space using a nonlinear transform (Brett, Leff, Rorden, & Ashburner, 2001). Peak voxels are reported in MNI coordinates. There were no significant activations which correlated, either negatively or positively, with the length of the stimulus.

RESULTS

We obtained both imaging and behavioral data from 15 right-handed native English speakers of English. The behavioral data established that although stems were

responded to faster [830 msec vs. 864 msec; $F(1, 190) = 38.22, p < .001$] than phrases (because they were shorter), there were no behavioral differences in the processing of nouns and verbs when length was factored out. For all stems together, there was no correlation between dominance and RTs [$r(192) = -.1, p > .1$] nor for the subset of stems that became NPs [$r(96) = -.14, p > .1$] or those that became VPs [$r(96) = -.06, p > .5$]. Similarly, there were no RT differences for the phrases [$r(192) = -.09, p > .2$].

In the analysis of the fMRI data, we included dominance scores as a parametric modulator. Parametric modulators are used in fMRI designs to model interactions between trial type (in this case, stem) and the covariate modeled as a modulator (in this case, dominance). Given that dominance is a continuous variable used to express the degree to which a stem is used as a noun or a verb, this is the most effective way of modeling this relationship. To the extent that nouns and verbs are represented in discrete neural regions, this should be evident in the effects of the parametric modulator. These different regions should correlate differentially with noun dominance and verb dominance. However, if nouns and verbs are not represented in distinct neural regions, there will be no differences in activation as a function of the frequency with which a word is used as a noun or a verb. We found that the stems activated the right cerebellum, the LIFG (BA 45,46,47), and the putamen (see Figure 2A and Table 2), but there was no effect of the dominance modulator. Contrary to the predictions of a modular account, there were no areas that increased or decreased in activation as a function of the frequency with which a stem was used as a verb or a noun, at either the standard statistical threshold of $p < .001$, corrected for multiple comparisons or at a lower threshold of $p < .01$. We also found no differences in activation between the stems when we divided them into two sets, those which became NPs and those which became VPs.

The phrases produced a similar overall pattern of activity as the stems with significant clusters in the right cerebellum, the LIFG (BA 45,46,47), and the putamen (see Figure 2B and Table 2). However, whereas phrases compared to baseline produced activity in the left middle temporal gyrus (LMTG; peak voxel: $-52 -44 -4$), stems did not, even at a lower threshold of $p < .01$.

The process-driven account predicts that noun-verb differences will not emerge for bare stems but only when they occur in phrasal contexts. We first determined whether there were differences in neural activation for all phrases compared to all stems. By comparing each set of stimuli to its appropriate length-matched baseline, we factored out the effects of differences in length between the phrases and the stems. Phrases generated greater activation compared to stems in the LMTG (BA 21), in the right middle occipital gyrus, and in

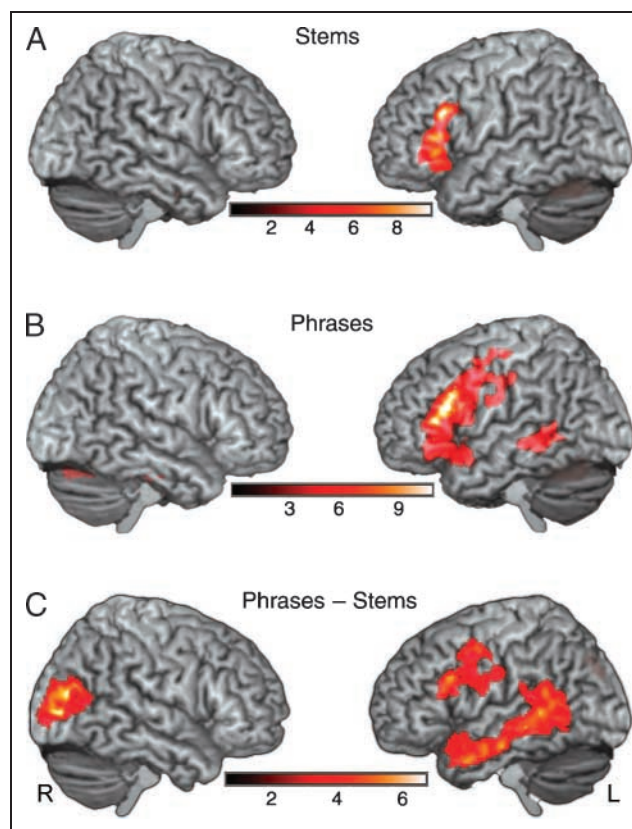


Figure 2. Differential brain activations generated by phrases and stems. Brain areas showing activations resulting from: (A) all stems, (B) all phrases, and (C) phrases minus stems. All analyses included comparisons against length-matched baselines to factor out effects of differences in length between stems and phrases. Activations were rendered at $p < .01$, voxel-level uncorrected, and $p < .05$, cluster-level corrected, for the entire brain. They were superimposed on a single subject's spatially normalized, 3-D-rendered T1-weighted image. The color bars indicate strength of activation (t scores). Phrases activated the left frontal and middle temporal cortices over and above stems.

the bilateral precuneus. At a lower threshold of $p < .01$, the LMTG activity consisted of a large swathe of activation running along its entire extent (see Figure 2C and Table 3) and there was also significant activity in the LIFG (BA 44,45,46) and the anterior cingulate. The dominance modulator had no effect on activity generated by phrases. There were no regions which were significantly more active for stems compared to phrases, even at a lower threshold. VPs compared to stems (taking the different baselines into account) produced significant activity in the LMTG (BA 21,22) and the right middle occipital gyrus, and in the LIFG at a lower threshold of $p < .01$, whereas NPs compared to stems only activated the LMTG, and the right middle occipital gyrus at a lower threshold (see Figure 2C and Table 3).

In the critical contrast between VPs and NPs, VPs produced greater activation in the left posterior MTG (LpMTG, BA 22, 39), extending into the left superior temporal gyrus (LSTG; peak voxel: $-52 -58 6, 127$ voxels;

Table 2. Peak Areas of Activity for the Contrasts of (A) Stems Minus Baseline, (B) Phrases Minus Baseline, (C) Noun Phrases Minus Baseline, and (D) Verb Phrases Minus Baseline

Region	Cluster		Cluster Level		Coordinates		
	BA	Extent	$p_{corrected}$	z Value	x	y	z
<i>(A) Stems Minus Baseline</i>							
LIFG	44	848	.000	5.20	-48	22	28
R Cerebellum		408	.000	4.38	20	-52	-32
L Putamen		159	.020	3.62	-30	-8	-4
<i>(B) Phrases Minus Baseline</i>							
LIFG	44	1608	.000	5.48	-52	20	28
L Putamen		275	.000	4.29	-28	-2	-6
LMTG	21	199	.004	3.95	-52	-44	-4
<i>(C) Noun Phrases Minus Baseline</i>							
LIFG	45/46	1131	.000	4.91	-50	30	12
LMTG	21	125	.002	3.86	-54	-44	-2
Putamen		133	.001	3.84	-32	4	-4
<i>(D) Verb Phrases Minus Baseline</i>							
LIFG	44	1859	.000	5.84	-52	20	28
Putamen		347	.000	4.54	-30	-6	-6
LMTG	21	272	.001	3.97	-52	-42	-4
R Cerebellum		109	.058	3.91	18	-54	-28

Voxel-level threshold of $p < .001$, uncorrected with a random field corrected p value of $p < .05$ for clusters adjusted for the entire brain (MNI coordinates).

Figure 3A and Table 4), whereas no regions were more strongly activated for NPs, even at a lower threshold.

DISCUSSION

The results from the fMRI study demonstrate that nouns and verbs *qua* nouns and verbs are not represented in separate regions of the brain. We found that stems which can function as nouns or verbs activated the same neural system; they did not generate differential activity simply as a function of their preference of use as a noun or verb (see also Tyler et al., 2001). However, when the grammatical differences between them are engaged by placing them in appropriate grammatical environments, where they serve different grammatical functions as nouns or verbs, we see differential patterns of neural activity, with stronger activation for verbs compared to nouns in the LpMTG.

In previous studies, the LpMTG has also been associated with the grammatical processing of sentences (Rodd, Longe, Randall, & Tyler, 2004; Tyler et al., 2001; Stowe et al., 1998), although activity in this region typically co-occurs with activity in the LIFG. In Rodd

et al. (2004), for example, processing spoken sentences activated both the LIFG and the LMTG, but the specific region of the LMTG which was activated varied as a function of whether the syntactic or semantic aspects of sentences were probed. Only syntactic analysis produced activity in the LIFG and in those posterior regions of the LMTG which were activated by VPs in the present study. In contrast, semantic processing generated activity confined to the mid-portion of the MTG, which did not extend posteriorly. Moreover, functional connectivity analyses on the fMRI data revealed distinct patterns of fronto-temporal connectivity for the two types of linguistic computation. Only syntactic processing showed fronto-temporal modulation involving the LIFG and the LpMTG. Functional connectivity during semantic processing involved the LIFG and the more anterior aspects of the LMTG (Tyler & Marslen-Wilson, 2008). The finding that the LIFG and the LpMTG are activated both for syntactic processing of sentences and for the processing of VPs in the present study suggests that they

Table 3. Brain Areas of Activity for the Contrasts of (A) Phrases Minus Stems, (B) Stems Minus Phrases, (C) Noun Phrases Minus Stems, (D) Stems Minus Noun Phrases, (E) Verb Phrases Minus Stems, and (F) Stems Minus Verb Phrases

Region	Cluster		Cluster Level		Coordinates		
	BA	Extent	$p_{corrected}$	z Value	x	y	z
<i>(A) [Phrases – Baseline] – [Stems – Baseline]</i>							
LMTG	21	616	.000	4.45	-46	-36	-6
R MOG	19	266	.000	4.32	32	-82	4
<i>(B) [Stems – Baseline] – [Phrases – Baseline]</i>							
No significant activations at $p = .001$ or $.01$							
<i>(C) [Noun Phrases – Baseline] – [Stems – Baseline]</i>							
LMTG	21	259	.000	3.96	-50	-32	-6
<i>(D) Stems – Noun Phrases</i>							
No significant activations at $p = .001$ or $.01$							
<i>(E) [Verb Phrases – Baseline] – [Stems – Baseline]</i>							
R MOG	18	406	.000	5.05	30	-88	6
LMTG	21	1191	.000	4.71	-46	-36	-6
LIFG	44	254	.000	4.22	-52	18	28
L Precuneus	7	127	.021	4.39	-12	-48	40
L Precuneus	31	215	.001	3.98	-2	-76	22
<i>(F) Stems – Verb Phrases</i>							
No significant activations at $p = .001$ or $.01$							

Voxel-level threshold of $p < .001$ uncorrected with a random field corrected p value of $p < .05$ for clusters adjusted for the entire brain (MNI coordinates).

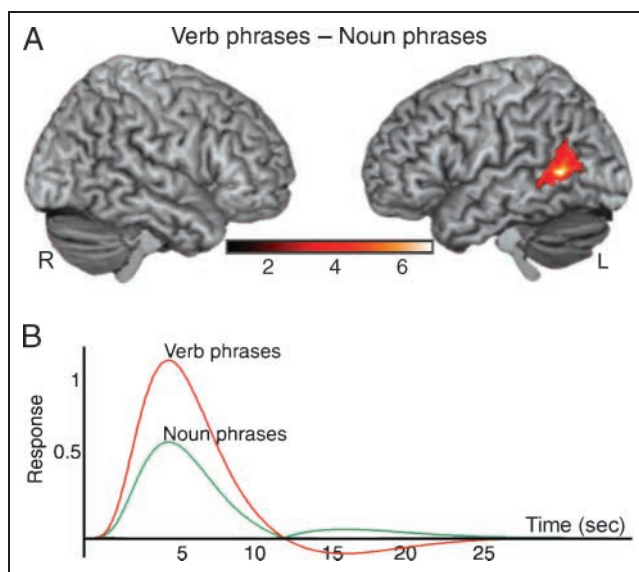


Figure 3. Differences in activation between VPs and NPs. (A) Brain areas showing significantly greater activation for VPs than for NPs in the LpMTG. Activations were rendered at $p < .01$, voxel-level uncorrected, and $p < .05$, cluster-level corrected, for the entire brain. Color bar indicates strength of activation (t scores). (B) Fitted peristimulus responses for VPs and NPs at the statistical peak in the left MTG (Talairach: $-52, -58, 6$).

engage the same neural network. In contrast, activation due to processing the semantic aspects of sentences did not extend to the posterior temporal cortex but instead was confined to the mid-portion of the LMTG (Rodd et al., 2004), a pattern similar to that obtained for NPs in the present study.

Supporting the claim for the role of the LpMTG in syntactic processing, previous studies have shown that damage to this region is associated with syntactic impairments (Tyler & Marslen-Wilson, 2008; Wilson & Saygin, 2004; Caplan, Hildebrandt, & Makris, 1996), suggesting that greater activity in this region in the present study reflects its involvement in the syntactic aspects of verb processing. Additional support for this interpretation comes from data from three patients with brain damage to posterior brain regions (Figure 4). We ob-

Table 4. Brain Areas of Activity for the Contrasts (A) Verb Phrases Minus Nouns Phrases and (B) Noun Phrases Minus Verb Phrases

Region	BA	Cluster Extent	Cluster Level		Coordinates		
			$p_{corrected}$	z Value	x	y	z
<i>(A) Verb Phrases – Noun Phrases</i>							
LMTG	39	127	.037	4.70	-52	-58	6

(B) Noun Phrases – Verb Phrases

No significant activations at $p = .001$ or $.01$

Voxel-level threshold of $p < .001$ uncorrected with a random field corrected p value of $p < .05$ for clusters adjusted for the entire brain (MNI coordinates).

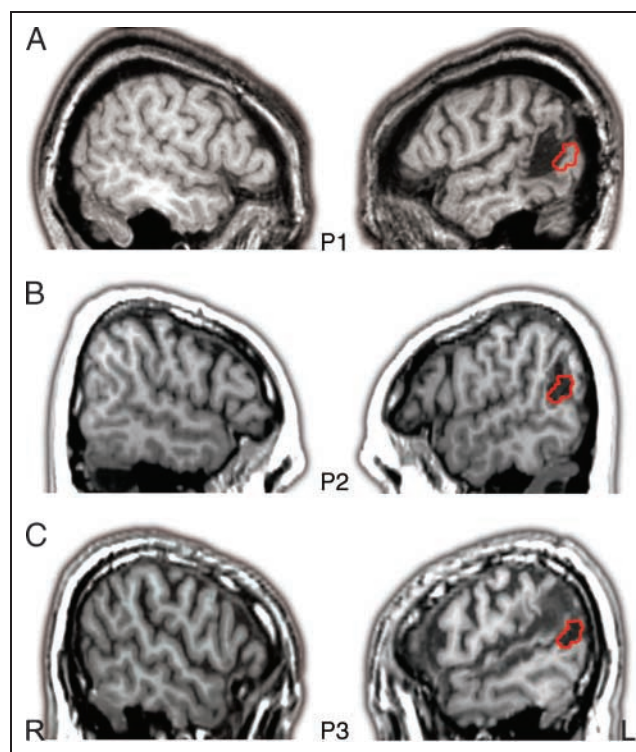


Figure 4. High-resolution T1-weighted 3-D rendered images for three brain-damaged patients. The scans show the stroke-induced lesions in the LpMTG. The outline of the activation for VPs versus NPs from Figure 3A is shown superimposed on the patients' brains. For P2 and P3, there is a substantial overlap between the activation site and the lesions, but not for P1 (see text).

tained magnetic resonance structural scans for each patient and extensively tested them on a variety of language tests. Two of the patients (P2, P3) had lesions in the LpMTG, which strikingly overlapped with the greater activity for VPs compared to NPs, but the third (P1) did not. Whereas P1 had no detectable language deficit, the latter two patients had a persistent and severe stroke-induced grammatical deficit, as revealed in several tests of grammatical processing (Tyler & Marslen-Wilson, 2008). For example, one of the tests we used, which is standardly employed for testing grammatical deficits in aphasia, is the reversible sentence test (e.g., Caramazza, Capasso, Capitani, & Miceli, 2005; Tyler et al., 2002). This is a sentence–picture matching test in which participants hear a spoken sentence, such as “the woman pushed the girl,” where either person can plausibly carry out the action. The subject’s task is to match the sentence to the correct picture in an array of three pictures, one of which is correct, a second contains a protagonist not mentioned in the sentence (e.g., a man instead of a woman), and a third reverses the roles of the protagonists (e.g., it shows the girl pushing the woman). Although the patients clearly knew the meaning of the words in the sentence (because they made few lexical errors), they could not appreciate the relational functions of the

verbs. They made a large number of errors (35%, 22%) which were always of the same type, where they chose the incorrect agent for the action. Hearing the sentence “the woman pushed the girl,” they incorrectly chose the picture which depicted the girl pushing the woman, indicating a specific inability to process the relational implications of verbs. Such errors are rare for healthy age-matched participants (Caplan et al., 1996), but reliably show up in patients who have deficits in grammatical processing. The patients’ grammatical deficit, accompanied by lesions in the same location as the region activated for VPs in the fMRI study, suggests that this region is differentially engaged in processing the syntactic implications of verbs when they occur as syntactic phrases.

The claim that damage to the LpMTG adversely affects syntactic processing is at odds with those views of the neural language system which stress the singular importance of regions of the LIFG (Broca’s area) in syntactic analysis (Grodzinsky, 2000). However, recent research using a combination of neuropsychological and neuroimaging data suggests a move away from models of functional specialization within the neural language system and toward a model in which different types of linguistic analyses are achieved by means of differential modulation within the fronto-temporal language system (Tyler & Marslen-Wilson, 2008; Stamatakis et al., 2005). This is more consistent with the view that syntactic impairments arise as a consequence of damage to either the LpMTG or the LIFG or to the connections between them (Caplan et al., 1996).

The finding, in the present study, that nouns and verbs activate different neural regions when their different linguistic functions are marked, is consistent with those previous findings which show neural differentiation for nouns and verbs when they are presented in linguistically marked contexts; in this case, when they are inflected (e.g., Longe et al., 2007; Tyler et al., 2004; Perani et al., 1999). In Longe et al. (2007), where we compared noun and verb stems with their inflected forms, we found greater activity for inflected verbs compared to inflected nouns in the LIFG and the LMTG, but no differences for noun and verb stems. Similarly, in a recent fMRI study comparing the processing of regularly and irregularly inflected words, we found greater activity for regularly inflected words in the LIFG and the LMTG. We argued that these regions formed a neural network involved in segmenting the inflected form into its stem and affix so triggering the linguistic functions carried by the affix (Tyler et al., 2005). Although the regions of the LMTG did not exactly overlap in the two studies—the LMTG activity for inflected verbs was slightly more medial than the activity for VPs seen in the present study—the fact that adjacent regions were activated in the two studies suggests that these adjoining regions of the LMTG may play related roles in mediating combinatorial linguistic processes. Taken together,

these results show that the neural language system is differentially sensitive to syntactic function whether it is marked intralexically (as in the case of inflected words) or extralexically (as is the case in phrases).

The lack of region-specific activation as a function of form-class per se may explain why previous lesion-behavior associations do not produce a consistent relationship between lesion location and behavioral deficits for either nouns or verbs. Across studies, there is considerable variation in the types of stimuli with which patients are tested, which may partially account for the inconsistency. Although some patients are tested with only noun and verb stems, others are tested on nouns and verbs in sentence or phrasal contexts (e.g., Silveri, Perri, & Cappa, 2003; McCarthy & Warrington, 1985). In addition, the mode of testing also varies, with some patients required to produce words, pictures, or sentences, whereas others are asked to comprehend them. Our results suggest that differences will emerge only when differences in the grammatical functions of nouns and verbs are marked and tested. Thus, patients may tend to show fewer noun-verb deficits when the stimuli involve uninflected stems which do not occur in a syntactic context than when the same words are either inflected or appear in grammatical contexts. These results, together with the finding that there were no regions more strongly activated for nouns compared to verbs, argue against those accounts that stress the separable neural representation of nouns and verbs. 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, nor does it generate differential patterns of activation. Instead, nouns and verbs are represented and processed within the same distributed neural language system, where behavior is modulated as a function of different types of linguistic analyses. The lack of neural segregation for nouns and verbs, and the focus on neural sensitivity to differences in linguistic process rather than linguistic content, may be illustrative of general principles that govern the neural representation of language organization in the brain.

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