

Neural processing of nouns and verbs: the role of inflectional morphology

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Abstract

Dissociations of nouns and verbs following brain damage have been interpreted as evidence for distinct neural substrates underlying different aspects of the language system. Some neuroimaging studies have supported this claim by finding neural differentiation for nouns and verbs [Brain 122 (1999) 2337] while others have argued against neural specialisation [Brain 119 (1996) 159; Brain 124 (2001) 1619]. We suggest that one reason why these inconsistencies may have arisen is because the morphological structure of nouns and verbs has been ignored. In an event-related functional magnetic resonance imaging (fMRI) study we test the hypothesis that the neural processing of nouns and verbs differs when they are inflected. We contrasted the processing of regularly inflected nouns (*dogs*) with regularly inflected verbs (*hitting*), and found that the LIFG was more strongly activated in processing regularly inflected verbs compared to regularly inflected nouns. Moreover, regions of LIFG that were more active in the fMRI study for inflected verbs partially overlapped with the lesions in patients who have particular problems with verb morphology. Taken together with previous studies, these results suggest that noun and verb stems do not differ in terms of their representation, but when verbs are morphologically complex they differentially engage those neural systems which are involved in processes of morpho-phonology and syntax.

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1. Introduction

There are many reports of brain-damaged patients who have disproportionate problems with verbs while nouns are relatively spared (Breedin, Saffran, & Schwartz, 1998; Goodglass, Klein, Carey, & Jones, 1966; McCarthy & Warrington, 1985; Miceli, Silveri, Villa, & Caramazza, 1984; Rapp & Caramazza, 1997) as well as some patients showing the reverse impairment (Damasio & Tranel, 1993; Zingeser & Berndt, 1990). This double dissociation is often associated with different neuropathology. In general, verb deficits accompany damage to the L frontal cortex while noun deficits arise from damage to the L temporal lobe. This behaviour–lesion association has been interpreted as showing that nouns and verbs are represented as grammatical categories in distinct neural substrates (Shapiro & Caramazza, 2003). However, verbs and nouns differ along

a number of dimensions and thus the cause of the dissociation remains unclear. On some accounts, the basis of the difference between nouns and verbs lies in their semantic representations, with nouns being more concrete and/or having more perceptual features than verbs (Breedin et al., 1998; Marshall, Chiat, Robson, & Pring, 1996a; Marshall, Pring, Chiat, & Robson, 1996b). Other accounts claim that they differ primarily in terms of their grammatical roles in sentences (e.g., Saffran, Schwartz, & Marin, 1980) or in terms of their lexical functions (e.g., Shapiro & Caramazza, 2003).

One important factor that is often overlooked in studies of noun/verb differences is differences in their morphological structure. Although there are many studies of patients with morphological deficits and studies of patients with disproportionate deficits for nouns or verbs, the two are rarely brought together. However, morphology is another important area where nouns and verbs differ. In English, most verb stems are associated with a range of regular inflections; for example, the stem *jump* can be inflected in a variety of ways, such as *jump + ing*, *jump + ed*, *jump + s*. Only about 160

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English verbs do not participate in this regular inflectional paradigm; these irregular verbs are inflected in idiosyncratic ways in their past tense forms although other aspects of their inflectional paradigm follow the regular pattern [eg the verb *think*, *thinks*, *thinking*, *thought*]. Nouns can also be inflected, but only with the plural marker [*cup* + *s*; *glass* + *es*].

There are a number of reasons to expect differences in the processing of inflected nouns and verbs. First, they are distinguished in some linguistic theories such as Pollock's split inflection hypothesis (Pollock, 1989) where there are structural differences between tense and agreement, each forming a distinct functional category. Second, in the relatively small number of neuropsychological studies where the morpho-syntactic functions of nouns and verbs have been compared, some patients show greater difficulties with morpho-syntactic operations involving nouns compared to verbs (Shapiro, Shelton, & Caramazza, 2000), while other patients have been reported with the opposite problem (Goodglass, Christiansen, & Gallagher, 1993; Tsapkini, Jarema, & Kehayia, 2002). For example, Goodglass et al. found that in both production and comprehension tests, non-fluent aphasic patients performed better on English plural nouns than on inflected verbs, even third person singular verbs. Along the same lines, Shapiro, Pascual-Leone, Mottaghy, Gangitano, and Caramazza (2001) found that repetitive transcranial magnetic stimulation (rTMS) applied to the L frontal cortex in healthy subjects differentially affected verb production when the subject's task was to produce the third person plural and singular forms of verbs compared to the plural and singular form of regular nouns. These studies suggest that there may be different processes underlying the regular inflectional morphology for nouns and verbs, which can be differentially impaired following brain damage. Given that that verb deficits are often associated with damage to the LIFG (e.g., Bak, O'Donovan, Xuereb, Boniface, & Hodges, 2001; Miceli et al., 1984) as are morphological deficits (e.g., Marslen-Wilson & Tyler, 1997; Tyler, de Mornay Davies, Longworth, Randall, & Marslen-Wilson, 2002a; Ullman et al., 1997), this raises the possibility that the LIFG is preferentially involved in the processing of verb inflectional morphology.

Neuroimaging studies investigating the representation of nouns and verbs have not explicitly taken into account potential differences in their morphology. This may be part of the reason why neuroimaging studies have not presented a consistent account of the representation of nouns and verbs. Some studies have revealed distinct patterns of activation associated with verbs but not nouns (e.g., Perani et al., 1999; Tranel, Damasio, & Damasio, 1997) while other studies have shown no differences in the neural activation for nouns and verbs (Tyler, Russell, Fadili, & Moss, 2001; Warburton et al., 1996). However, these studies vary in the extent to which the task and/or the stimuli explicitly involve inflected words. For example, in the Warburton et al. study, subjects were required to generate verbs in response to concrete nouns or nouns in response to superordinate labels. There is

no way of knowing whether the subjects consistently produced stems or inflected words. In the Perani et al. study, subjects made lexical decision judgements to written nouns and verbs, and since the language used was Italian, all of the words were inflected. In contrast, in the Tyler et al. study, the verbs and nouns were all uninflected. Although it is not possible to draw any firm conclusions from these studies about potential differences in the role of inflectional morphology in processing nouns and verbs, one plausible hypothesis is that processing uninflected verbs and nouns engages the same neural system (Tyler et al., 2001) but differences are seen when inflected nouns and verbs are processed, with the LIFG being more strongly activated by inflected verbs compared to inflected nouns (Perani et al., 1999).

To determine whether there is differential neural activation for nouns and verbs when they are inflected, we carried out a functional magnetic resonance imaging (fMRI) study comparing the processing of regularly inflected nouns with regularly inflected verbs in English. We used a semantic categorisation task in which subjects viewed sequences of three words, consisting of either inflected nouns or verbs, and indicated whether the last word was semantically related to the first two words. By using this semantic relatedness task we ensured that the subject's attention was not directed towards the endings of the words, which was the variable of interest, thus making the task a more implicit test of inflectional processing. Activations for nouns and verbs were compared against activation in the baseline task in which subjects saw triplets of letter strings and indicated whether the target letter string was composed of the same or different letters as the cue string. The question here was whether we would obtain any differences when subjects were asked to process inflected nouns and verbs.

To test the hypothesis that it is damage to regions of the LIFG in aphasic patients that causes their problems in processing inflected verbs, we planned to compare the spatial extent of activations obtained in the present fMRI study with the lesion site in three patients who have documented problems with the regular past tense verbal morphology (Tyler et al., 2002a; Tyler, Randall, & Marslen-Wilson, 2002b), and whose deficit extends to other regular verbal inflections. Extensive overlap between lesion site in these patients and activations in healthy subjects while processing regular verbal inflections would lend further support to a primary role for LIFG in the processing of regularly inflected verbs.

2. Imaging study

2.1. Methods

2.1.1. Subjects

Twelve right-handed subjects aged 20–33 years (mean 24 years, eight males, four females) participated in this study. All gave informed consent. The study was approved by Addenbrookes NHS Trust Ethical Committee.

2.2. Materials

The materials consisted of two sets of items: regularly inflected nouns and regularly inflected verbs. The regularly inflected nouns were all -s suffixed forms while the verbs were all -ing suffixed. There were a total of 120 nouns and 120 verbs. Given the prevalence of form-class ambiguity in English, we applied a set of strict criteria in our selection of nouns and verbs. Most of the nouns (77%) were form-class unambiguous, as determined by the CELEX database. Where it was not possible to select an unambiguous noun, we chose nouns whose stem frequency was significantly higher as a noun than as a verb [mean lemma frequency as noun = 9; mean lemma frequency as verb = 1] and whose wordform frequency was also significantly higher as a plural noun than as a third person singular verb [mean wordform frequency as plural noun = 3; mean wordform frequency as third person singular verb = 0]. Thirty percent of the verbs were formclass unambiguous. Of the remainder, the stem frequency was much higher as a verb than as a noun [mean lemma frequency as verb = 39; mean stem frequency as noun = 10] and the wordform frequency was also significantly higher as a verb than as either a noun or adjective [mean wordform frequency as verb = 12; mean wordform frequency as noun/adjective = 0].

The sets of nouns and verbs were arranged into triplets consisting of two cue words followed by a target word. One set consisted of triplets of regularly inflected verbs (*eating*, *grazing*, *DINING*) while the other consisted of triplets of plural nouns (*sparrows*, *thrushes*, *WRENS*). In half the trials the target was semantically related to the two preceding cue words and in the other half it was unrelated (e.g., *ravens*, *canaries*, *WEASELS*; *talking*, *speaking*, *LEAPING*). We used a completely counter-balanced design in which each word appeared as a cue word in position 1, position 2, and as a related target and unrelated target across sessions. To ensure that the triplets in the semantically related noun and verb conditions were judged to be equally related, we ran a separate study in which 15 subjects were presented with each triplet and asked to judge the degree to which the target was semantically related to the pair of cue words, using a scale of 1–7 where 1 was very unrelated and 7 was very related. The mean ratings for related nouns (6.1) and verbs (6.0) did not differ significantly.

The subject's task was to press one response button if the target was semantically related to the two cue words, and another button if they were unrelated. We included a baseline condition, consisting of triplets of single letter strings (e.g., kkkk, kkkkkkk, KKKKK; ttt, tttt, MMMM) matched on letter length and case to the individual test trials. The cues were in lower case and the targets were in upper case. Subjects pressed one response button if the target letter string was composed of the same letters as the cues and a second button if they were different. The baseline and experimental tasks shared many of the same task components, but differed in the type of stimuli delivered to the subject. Both test and

baseline trials required subjects to process the visually presented stimuli and make a decision about the relationship between the target and the cue words and press a response key. We chose this paradigm since it has been successfully used to explore issues involved in processing written words in other studies using both PET and fMRI (Devlin et al., 2002; Tyler et al., 2001).

Test and baseline trials were pseudo-randomly organised into two sessions. Thirty practise trials (10 baseline and 20 test items) preceded the test trials.

2.2.1. Procedure

Subjects saw sequences of three written words (two cues plus target) presented visually, one at a time, via computer and projected to a mirror directly above their head, at eye-level. Cue words were presented in lower case and targets in upper case.

Each of the three words or letter strings was presented for 200 ms with a between-item delay of 400 ms. The target item was followed by a delay of 3 s. Each event (triplet of words/letter strings) lasted for 4.4 s. The event duration was not an integer multiple of the TR (3 s) and therefore data was sampled at various points along the HRF ensuring an effective sampling rate (Josephs, Turner, & Friston, 1997). The same timing parameters were used for both the semantic and baseline tasks.

Scanning was carried out on a 3 T Bruker Medspec Avance S300 system at Wolfson Brain Imaging Center, Cambridge, England, using a gradient-echo EPI sequence (TR = 3000 ms, TE = 30 ms, flip angle 90°, FOV 25 cm × 25 cm, 21 oblique slices, 4 mm thick (1 mm gap between slices, 128 × 128 in-plane resolution, 152 repetitions)) with head coils, 200 kHz bandwidth and spin echo guided reconstruction. T1-weighted scans were acquired for anatomical localisation.

3. Results

3.1. Behavioural analysis

Reaction times (RTs) to indicate whether the target was related or unrelated to the cue words were measured from the onset of the target word in each triplet. Since the nouns and verbs could not be perfectly matched on frequency and letter length (the verbs were slightly longer [there was on average eight letters in verbs and seven in the noun set] and more frequent than the nouns (see Section 2)) these factors were entered into an analysis of variance as co-variates. This analysis showed that there was no difference in reaction times to nouns and verbs ($F(1, 291) = 1.16, P = 0.282$), with the RT to nouns averaging 640 ms and verbs averaging 621 ms, confirming that the materials did not differ in processing difficulty. Similarly, there were no significant differences in error rates ($F(1, 316) = 2.36; P > 0.1$), with nouns averaging 4.5% errors and verbs averaging 5.5%.

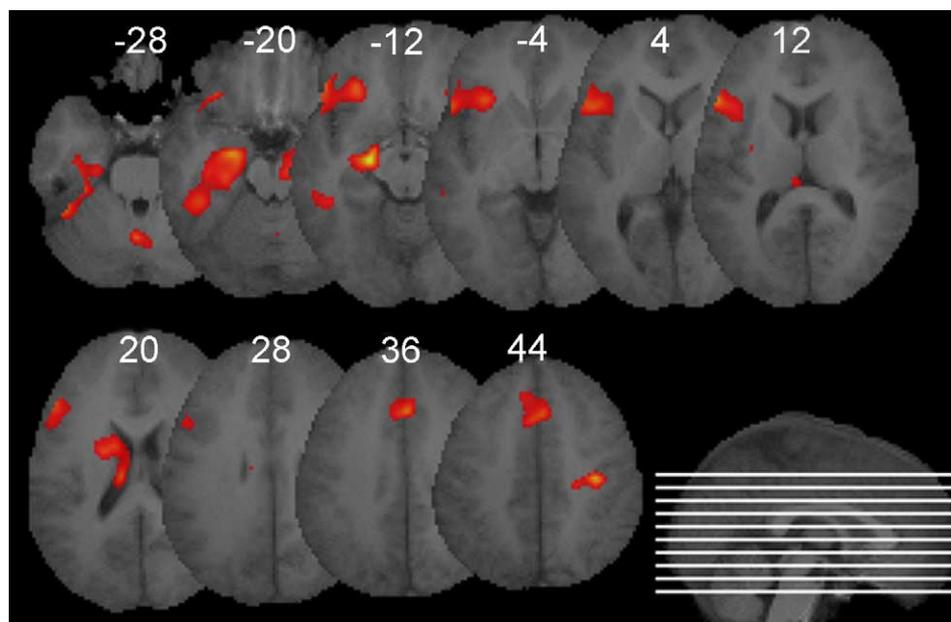


Fig. 1. Peak activation areas for the contrast of words minus baseline. Activations are shown superimposed on the mean image of the 12 subjects' T1 images. The areas shown in colour were reliably ($P < 0.05$) active after statistical correction.

3.2. Analysis of fMRI data

Data analysis was performed using SPM99 software (Wellcome Institute of Cognitive Neurology, <http://www.fil.ion.ucl.ac.uk>), implemented in Matlab (Mathworks Inc. Sherborn, Mass., USA). Pre-processing comprised initially of slice timing correction and image realignment to account for different slice acquisition times and head motion. The images were then spatially normalised to a standard EPI template based on the Montreal Neurological Institute (MNI) reference brain, using $7 \times 8 \times 7$ nonlinear basis functions. The spatially normalised images were smoothed with an isotropic 12 mm full-width half-maximal Gaussian kernel. We used a 12 mm smoothing kernel, suitable for random effects analysis, as a way of correcting for anatomical variation across subjects (Xiong et al., 2000) and because we had no a priori reasons for expecting small regional differences as a function of noun/verb processing (Worsley & Friston, 1995). The data for each subject were modelled using the general linear model (Friston et al., 1995). Four sessions and five variables were entered into the model (verbs, nouns and baseline).¹ The BOLD response for each event was modelled with the canonical haemodynamic re-

sponse function (HRF). The first six scans of each time series were discarded to allow for T1 equilibrium before the test trials started. The time-series in each voxel were highpass-filtered to remove low-frequency noise and scaled to a grand mean of 100 over all voxels and scans within each session. Since the sets of verbs and nouns could not be matched on frequency and letter length, these variables were entered as parametric modulators (with linear expansion). Contrast images from each subject were combined into a group random effects analysis. Results were thresholded at $P < 0.001$ uncorrected and only clusters that survived $P < 0.05$ corrected for multiple comparisons across the entire brain volume were considered significant. We report maximum cluster peaks in the Tables and describe cluster extents in the text. Since SPM coordinates are given in Montreal Neurological Institute (MNI) space, regions were identified by converting the coordinates to Talairach space with a nonlinear transform (Brett, 2001).

We used SPM to detect those brain regions that were activated for words compared to baseline, and for the direct contrasts between verbs and nouns. Comparing words (nouns & verbs combined) against baseline (Fig. 1 and Table 1), we found significant activation of the primarily LH frontal/temporal system that is typically activated in neuroimaging studies of lexical-semantic processing (Vandenberghe, Price, Wise, Josephs, & Frackowiack, 1996). Specifically, there were several significantly ($P < 0.05$ corrected for multiple comparisons) activated clusters. The cluster with the most significant peak activation was in the left parahippocampal gyrus (BA 28, 34, 35, 36) including the left fusiform gyrus (BA 20, 37) and the hippocampus. This region has been associated with high relative to low level semantic association demands in fMRI

¹ Aspects of these data have previously been reported (Tyler et al., 2003a) where we contrasted two types of verbs (animate and inanimate movement) and two types of objects (animate and inanimate) to examine biological and non-biological semantic representations. This distinction was not relevant in the current analysis. However, to determine whether the animacy variable affected noun-verb activation, we carried out further analyses in which we contrasted [animate nouns + inanimate nouns] – [animate verbs + inanimate verbs]. The interaction was not significant, showing that the animacy variable did not interact with the noun-verb difference.

Table 1
Coordinates of peak activations for the contrast of words minus baseline

Regions	Cluster level		Voxel level		Coordinates		
	$P_{\text{corrected}}$	Extent	$P_{\text{corrected}}$	t	x	y	z
L parahip gyrus (BA 37)	0.000	1397	0.004	13.78	-20	-14	-14
L parahip gyrus (BA 36)			0.329	7.21	-34	-26	-26
L fusiform gyrus (BA 37)			0.345	7.15	-42	-46	-28
R precentral gyrus (BA 4)	0.024	170	0.109	8.71	38	-20	44
R cingulate gyrus (BA 24)			0.89	5.39	26	-22	42
L inf. Frontal gyrus (BA 45)	0.000	1631	0.198	7.91	-50	22	10
L inf. Frontal gyrus (BA 47)			0.223	7.75	-28	24	-8
L inf. Frontal gyrus (BA 47)			0.375	7.03	-50	18	-6
R cingulate gyrus (BA 32)	0.000	527	0.244	7.62	4	22	34
L medial frontal gyrus (BA 6)			0.525	6.52	-2	14	48
L medial frontal gyrus (BA 8)			0.983	4.77	-4	28	46
R cerebellum, ant. lobe	0.005	246	0.335	7.19	4	-62	-26
R cerebellum, post. Lobe			0.668	6.1	10	-76	-34
L thalamus	0.000	456	0.466	6.71	-8	-18	20
L caudate, caudate body			0.617	6.25	-18	-4	20
L thalamus			0.963	4.98	-2	-28	12
R inf. Frontal gyrus (BA 47)	0.029	162	0.536	6.49	34	26	-12
R brainstem, midbrain	0.015	192	0.734	5.91	12	-22	-22

Coordinates presented in MNI space. L, left; R, right; inf., inferior; ant., anterior; post., posterior; parahip., parahippocampal.

(Ricci et al., 1999), and semantic categorisation of words and lexical decision effects in PET (Devlin et al., 2002). The cluster extended inferiorly to the cerebellum and superiorly to the left middle temporal gyrus (BA 21). Due to susceptibility artefacts we may be underestimating activation in rostral temporal cortex. A second cluster centred in the right precentral gyrus (BA 3, 4) and included the postcentral gyrus (BA 3) and the right cingulate gyrus (BA 24), areas associated with verbal encoding or recognition processes (e.g., Baker, Sanders, Maccotta, & Buckner, 2001; Heun et al., 1999). A third cluster peaked in the left inferior frontal gyrus (BA 45, 47) and included the insula, extending posteriorly to the left superior temporal gyrus (BA 38), regions which are activated for a wide range of tasks, processes and materials. For example, this region is activated during semantic association or categorisation tasks involving words (for reviews see Bookheimer, 2002; Price, 2000). It has also been identified as part of a semantic encoding network necessary for successful memory formation (Fletcher et al., 1995; Wagner et al., 1998), as a component of a fronto-parietal network subserving verbal working memory (Honey et al., 2002; Smith & Jonides, 1999), and it has been associated with semantic retrieval (Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997). A cluster in the anterior cingulate included the left and right cingulate gyrus (BA 32), extending to left and right medial frontal gyrus (BA 6, 8), possibly related to aspects of working memory rather than semantic processing per se (e.g., Carter, Botvinick, & Cohen, 1999; Cowell, Egan, Code, Harasty, & Watson, 2000; Sylvester et al., 2003). There were also clusters in the cerebellum, left thalamus/caudate

and right inferior frontal gyrus (BA 47). Finally there was a cluster with peak activation at the right brainstem that included the right parahippocampal gyrus (BA 28, 34), and the amygdala.

The comparison of nouns minus baseline showed significant activation in left parahippocampal gyrus (BA 28, 34, 36) including the left fusiform gyrus (BA 37), inferior temporal gyrus (BA 37) and left inferior frontal gyrus (BA 45, 47) including the anterior insula and extending into the left middle frontal gyrus (BA 9). Comparing verbs against the baseline produced significant activation in LIFG (areas pars triangularis and orbitalis; BA 45, 47), including the left insula and the left precentral gyrus, left parahippocampal gyrus (BA 28, 34, 36) including the left fusiform gyrus (BA 20, 37) and middle temporal gyrus (BA 22). There were also clusters in the anterior cingulate which included left and right cingulate gyrus (BA 32).

The critical analysis involved the direct comparison between verbs and nouns, where we found that the only significant difference was in LIFG, where the verbs significantly activated a large cluster in L inferior frontal cortex (areas 44, 45, 47). The anterior to posterior extent was relatively narrow, encompassing primarily the posterior portion of the inferior frontal gyrus and also the insula. Relative to the baseline condition, verbs showed greater activation than nouns throughout this area of LIFG, as shown by the signal change plots in Fig. 2 and Table 2. These show plots of the activation for verbs minus baseline and nouns minus baseline at the significant activation peaks. In addition, we also sampled throughout the LIFG and report these plots in the figure. In the reverse contrast (nouns–verbs), nouns did not

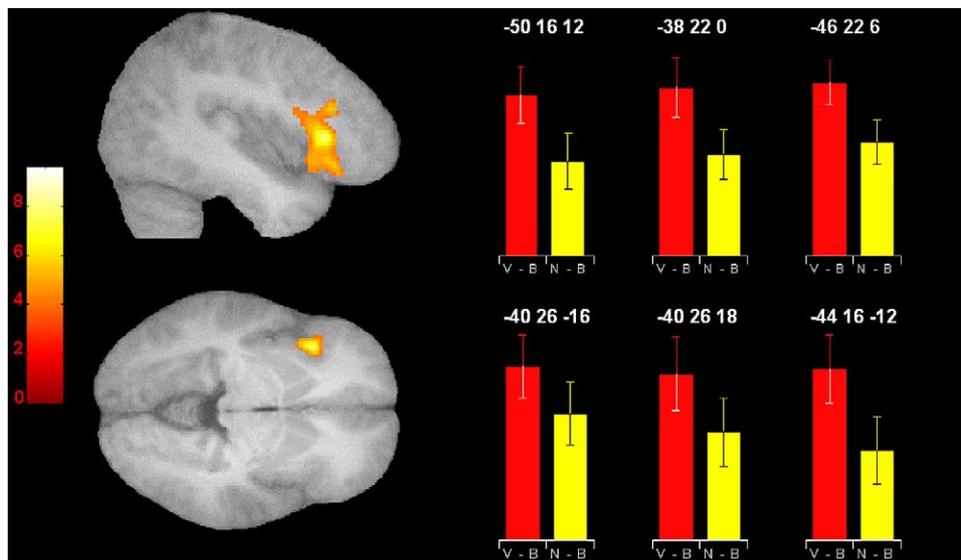


Fig. 2. The areas activated in the verbs–nouns contrast. Activations are shown superimposed on the mean image of the 12 subjects' T1 images. The areas shown in colour were reliably ($P < 0.05$) active after statistical correction. The plots show signal change within the region of activation for verbs (V) against baseline (B) (red) and nouns (N) against baseline (B) (yellow). The upper plots show signal change at activation peaks in the verbs–nouns contrast. The lower plots show signal change at randomly sampled points across the verbs–nouns cluster. Cluster extents are thresholded at $P = 0.001$ uncorrected.

significantly activate this, or any other region, more than verbs, even when we lowered the statistical threshold to 0.01 uncorrected, with only clusters that survived $P < 0.05$ corrected for multiple comparisons across the entire brain volume considered significant. However, it is clear from the nouns–baseline contrast that nouns do activate LIFG, but the contrast analysis shows that verbs activate it significantly more than do the nouns.

In summary, both nouns and verbs activate regions of inferior temporal cortex to a similar extent, suggesting that there were no differences in the degree to which their semantic representations were activated, supporting our earlier claims made on the basis of our previous PET study with noun and verb stems (Tyler et al., 2001). However, there were clear and significant differences in the frontal cortex, with verbs activating this region significantly more than nouns.

3.2.1. Effects of frequency and letter length

As noted above, we were unable to fully match the noun and verb sets on letter length and word frequency; the nouns were slightly shorter than the verbs and the verbs were slightly more frequent than the nouns. Previous stud-

ies have suggested that variables such as frequency and word length may place differential demands on working memory (Baddeley, Thompson, & Buchanan, 1975; Balota & Spieler, 1999). This account would predict that verbs, because they were slightly longer than nouns, may have engaged working memory processes to a greater extent than nouns. In contrast, the higher frequency of the verbs would predict greater involvement of working memory during the processing of nouns relative to verbs. To control for the potential effects of these variables we entered them as co-variables (parametric modulators) in our imaging analysis, as described above. To determine whether the differential activations found in LIFG were due to differences in working memory involvement, we directly assessed the effects of word length and frequency, independently of other task elements. The results show that word frequency was not associated with activation in any brain region ($P = 0.001$ uncorrected for multiple comparisons) and that effects of word length during task performance were restricted to posterior brain regions (cuneus/lingual gyrus) in both hemispheres (see Fig. 3 and Table 3). No effects were observed in LIFG or parietal cortex. Thus, neither word length nor

Table 2
Coordinates of peak activations in the verbs–nouns contrast

Regions	Cluster level		Voxel level		Coordinates		
	$P_{\text{corrected}}$	Extent	$P_{\text{corrected}}$	t	x	y	z
L inf. Frontal gyrus (BA 44)	0.000	1040	0.046	9.59	−50	16	12
L inf. Frontal gyrus (BA 47)			0.081	8.83	−38	22	0
L inf. Frontal gyrus (BA 45)			0.100	8.55	−46	22	6

Coordinates presented in MNI space. L, left; inf., inferior.

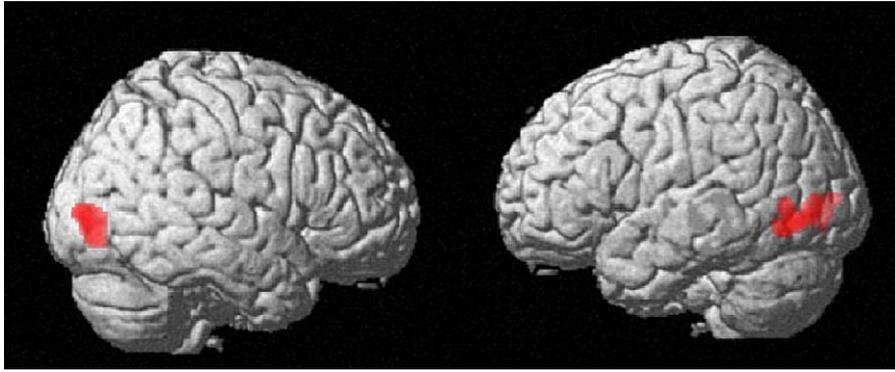


Fig. 3. Effects of the parametric modulator showing areas associated with word length. No significant effects were found for frequency. The clusters shown in red were reliably ($P < 0.05$) active after statistical correction. Cluster extents are thresholded at $P = 0.001$, uncorrected.

frequency in the present study appeared to engage the left fronto-parietal network associated with the phonological loop component of working memory (e.g., Coull, Frith, Frackowiak, & Grasby, 1996).

3.3. Relating activations to lesion site

The strong prediction raised by the current finding is that patients who have problems with inflected verbs will have damage to the same cortical region that is selectively activated for inflected verbs in the present study. To determine whether the region of LIFC which was activated for verbs in the present study overlaps with the cortical region that is typically impaired in brain-damaged patients with deficits in verbal morphology, we selected three right-handed aphasic patients who were able to have structural MR scans and who have documented problems in processing verb morphology. The language deficits of two of the patients have been reported previously (Tyler, 1992; Tyler et al., 2002a,b) while the third has been briefly discussed in Longworth, Marslen-Wilson, and Tyler (2002). Two patients (DE and CH) had L middle cerebral artery infarcts while the third (a 41-year-old woman, SD) had suffered an aneurysm and haematoma. In all cases, brain damage affected the LIFC and L superior temporal cortex. None of the patients were generally cognitively impaired; they all scored within the normal range on the Ravens Progressive Matrices. Two of the patients (DE, CH) showed a pattern of language deficit which is typical of non-fluent Broca's aphasics; slow and hesitant speech, intact single word repetition but impaired

repetition of sentences, reverse role errors on reversible sentences suggesting that they have syntactic difficulties, and normal performance on tests of semantics. The third patient (SD) did not have a discernible production deficit, nor did she make reverse role errors on reversible sentences indicating that she did not have a syntactic deficit. Moreover, she did not have a detectable semantic deficit; she made very few errors (5%) on a picture naming task (Bunn, Tyler, & Moss, 1998) and 4% errors on a property verification task (Moss, Tyler, & Devlin, 2002) and she shows normal semantic priming effects for uninflected words (Longworth et al., 2002). The language comprehension abilities of all of the patients were sufficiently intact for them to have no difficulty in understanding instructions and communicating with the experimenter.

All patients were previously tested in an experiment which investigates one aspect of verbal inflection—the difference between the regular and irregular past tense (Tyler et al., 2002a). In this study, we compared priming for regularly (*jumped-jump*) and irregularly inflected past tense (*brought-bring*) words, and for phonologically related (*gravy-grave*) and semantically related (*cherry-grape*) word-pairs. Healthy control subjects showed significant priming effects for both types of inflected words and for the semantically related pairs, but not for the phonologically related pairs (showing that the morphologically related pairs were not priming purely on the basis of form overlap). In all respects except one, the patients produced the same pattern as the control subjects; the exception was the lack of priming for the regularly inflected past tense

Table 3
Significant clusters associated with the effects of the parametric modular

Regions	Cluster level		Voxel level		Coordinates		
	$P_{corrected}$	Extent	$P_{corrected}$	t	x	y	z
L lingual gyrus (BA 19)	0.009	207	0.732	5.97	-26	-70	-6
L lingual gyrus (BA 19)			0.955	5.09	-18	-78	-2
R lingual gyrus/cuneus (BA 17/18)	0.013	192	0.586	6.39	16	-84	0
R cuneus (BA 17)			0.941	5.18	14	-92	6

Coordinates presented in MNI space. L, left; R, right.

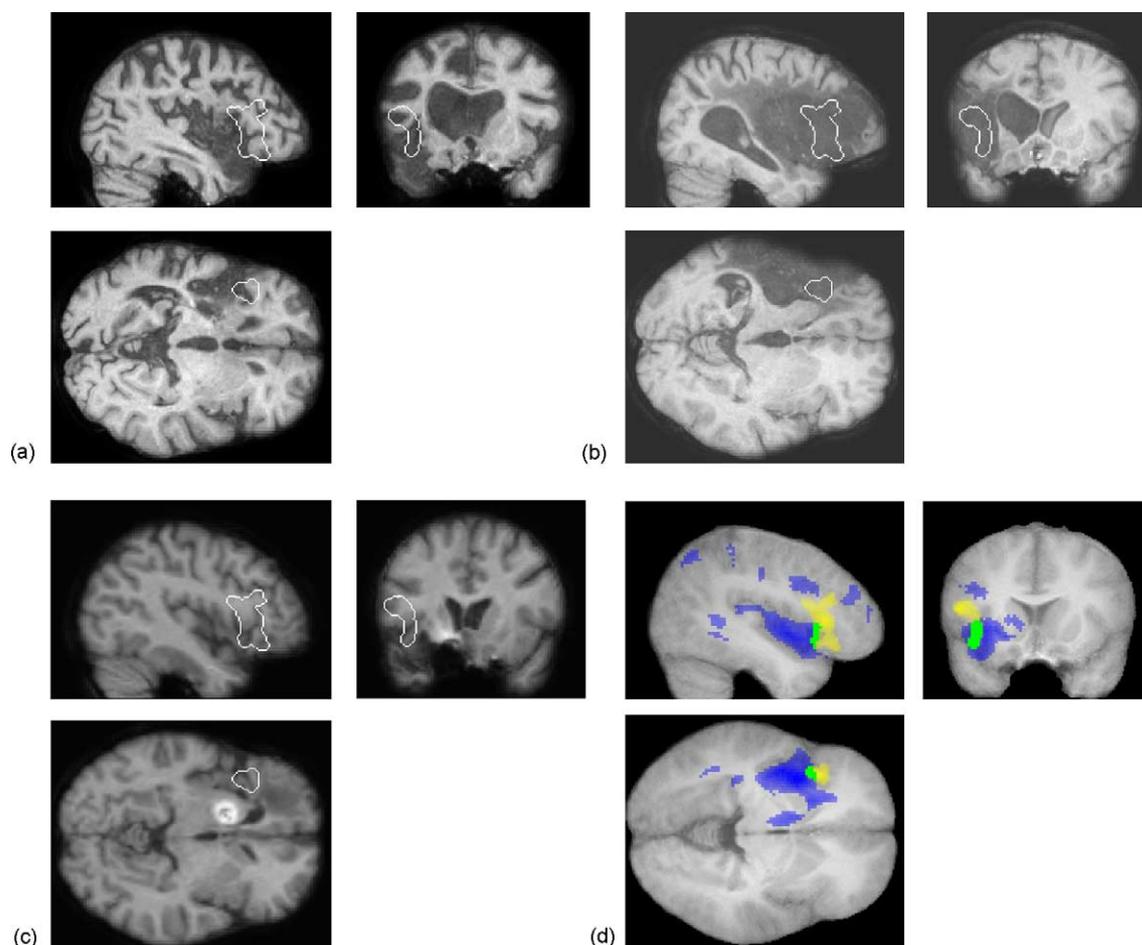


Fig. 4. (a–c) Show T1 images of three patients with an outline of the activation found in the verbs–nouns contrast (see Fig. 2) superimposed on them. All images are in Talairach space and were aligned with spatial normalisation in SPM99. (d) Shows a mean of the spatially normalised T1 images of the 12 subjects in the fMRI experiment overlaid with the lesion overlap of the three patients in (a–c). Lesion overlap is shown in blue, the significant activation found in the verbs–nouns contrast is in yellow (see Fig. 2), and the overlap between common lesion volume of the three patients and the activation is in green.

forms.² In a further study, we established that the patients' lack of priming for the regulars was not due to a generalised phonological deficit (Tyler et al., 2002b).³ Finally, we have recently shown that these patients show no semantic priming for regularly inflected past tense forms although they have no difficulty in activating the meaning of uninflected verb stems (Longworth et al., 2002).⁴ Taken together, these studies provide strong evidence that the three patients have problems processing regularly inflected past tense forms.

To determine directly whether these patients had more problems with the verbal inflection [-ing] compared to the noun inflection [-s] used in the present study, we obtained behavioural data from the patients on the task reported in this

paper. SD's response latencies in the inflected verb condition were significantly slower than in the inflected noun condition (nouns = 627 ms; verbs = 674 ms; $F(1, 152) = 4.85$, $P < 0.05$; verbs = 8% errors, nouns = 3.8% errors) as were DE's (nouns = 877 ms; verbs = 1124 ms; $F(1, 116) = 4.15$, $P < 0.05$; verbs = 15% errors, nouns = 6.3% errors). Although we were unable to obtain reliable RT data from CH, her error rates showed a similar pattern to the latency data from the other two patients; she made 13% errors on the related verbs and 0 errors on the related nouns. This was not the pattern shown by the healthy subjects, whose responses to verbs and nouns did not differ significantly (see Section 3.1). These results from the patients suggest that they also have problems with the type of verbal inflection which we used in the present imaging study.

Fig. 4a–c show T1 images of the three patients with an outline of the activation found in the verbs minus nouns contrast (see Fig. 2 and Table 2) superimposed on them. We used voxel-based morphometry (VBM, Ashburner & Friston, 2000) to identify the common areas of damaged

² The results from SD were obtained too late to be included in this paper. However, in this study, she showed a significant 75 ms priming effect for the irregulars and a 70 ms significant priming effect for the semantic condition. Neither the 27 ms priming for the regulars nor the –95 ms priming for the phonological condition were significant.

³ SD could not be tested on this study.

⁴ CH could not be tested on this study.

cortical tissue in all three patients. We first estimated the lesion extent using voxel-based VBM on the patient T1 images without the segmentation step, given the difficulties of segmentation with large lesions. Each patient image was spatially normalised to the Talairach space with 12 parameter linear affine transformations as implemented in SPM99. To avoid distorting the lesions (Brett, Leff, Rorden, & Ashburner, 2001) all nonlinear components (warping) were excluded from the spatial normalisation. A group of 32 control scans were spatially normalised following the same procedure. Each patient was compared to the group of 32 controls and the results were combined in a conjunction analysis to identify areas of common abnormality. We then overlaid the cluster that was selectively activated for verbs in the fMRI study (Fig. 2 and Table 2) onto the mean brain image. As Fig. 3 shows, the brain region selectively activated for inflected verbs falls within the common region of LIFC damage in these patients. Specifically, it involves the inferior frontal gyrus (BA 47) extending posteriorly and medially to the insula, and inferiorly to superior temporal gyrus (BA 38). There is a small area of overlap in BA 45.

4. Discussion

In the imaging study, we found robust activation for inflected nouns and verbs in the L frontal and temporal (inferior and lateral) cortices. These are the regions that are typically activated in imaging studies involving the processing of written words when the task involves semantic processing (e.g., Price et al., 1994; Rumsey et al., 1997). In the direct contrast between nouns and verbs, we found that only the LIFG was activated significantly more strongly for verbs compared to nouns. In additional analyses we ruled out the possibility that this stronger LIFG activation may have resulted from lexical differences between the nouns and verbs, such as word frequency or word length, which may have placed differential demands on working memory. Each of these variables is known to affect working memory demands where subjects are required to hold information in memory in order to carry out the task, as was the case in the present study. In an analysis of the influence of these two variables, we found that the effect of word length was confined to regions of occipital cortex, reflecting greater visual processing required for longer words, and did not involve the LIFG. Likewise, the LIFG was not modulated by the variable of word frequency. Moreover, given that working memory usually activates a more extensive neural system, involving parietal as well as frontal cortex (Gruber & von Cramon, 2001; Awh et al., 1996; Fletcher & Henson, 2001), it is unlikely that the observed increased activation for verbs in the LIFG was due to increased working memory demands.

How do the present results relate to previous imaging studies exploring possible formclass differences? Most studies have employed the verb generation task in which subjects are asked to generate a verb in response to a noun (Buckner,

Koustaal, Schacter, & Rosen, 2000; Petersen, Fox, Posner, Mintun, & Raichle, 1989; Warburton et al., 1996). As we have pointed out previously (Tyler et al., 2001) this task conflates the joint contribution of noun and verb processing to neural activation, since both nouns and verbs are involved on each trial. One of the few imaging studies that separated the processing of nouns and verbs used a lexical decision task (Perani et al., 1999), and found additional activation in LIFC for verbs compared to nouns. Although Perani et al. claim claimed that their results show that regions of LIFC are specifically engaged by verb processing, their data actually show differential degrees of activation for nouns and verbs in the same cortical region. This is consistent with the present results, given that both studies use inflected nouns and verbs. The Perani et al. study was conducted in Italian, a language in which verbs and nouns are obligatorily inflected and which does not allow verb or noun stems to occur in isolation. For example, a typical verb used in the Perani et al. study was *to cut*, which is *tagliare* [*tagli* + *are*] in Italian. The stem *tagli* is not a real word and cannot stand alone like verb stems in English. Similarly, the noun *hammer* is *martello* [*martell* + *o*] in Italian, and the stem *martell* is a non-word. This makes the Perani et al. study comparable to the present experiment since both studies use inflected words.

In contrast, when nouns and verbs are not inflected, they seem to activate the same neural system to the same extent. This was clearly shown in a previous study involving the same semantic categorisation task as used in the present experiment and comparing processing of noun and verb stems (Tyler et al., 2001), where we found robust activation in LIFG and L temporal cortex for both nouns and verbs with no significant differences between them. Taken together, these findings are most compatible with the view that nouns and verbs are represented in the same unitary distributed fronto-temporal network rather than in a categorically organised neural system, but that the processing of inflected verbs preferentially engages the LIFG in both Italian and English.

What might be the basis for the greater involvement of LIFG activity during the processing of inflected verbs? It is unlikely that inflected verbs are simply harder to process than inflected nouns since there were no significant RT or error differences between the two word-types, either in or out of the scanner. One possibility relates to recent claims that have been made about the role of the LIFG in processes of selection (Thompson-Schill, D'Esposito, & Kan, 1999; Wagner, Pare-Blagoey, Clark, & Poldrack, 2001). The proposal here is that regions of the LIFG are involved when the task involves selecting among competing alternatives. Although most of the evidence supporting this proposal has involved semantic selection, Thompson-Schill et al. (1997) suggest that demands on prefrontal cortex may be increased by any "task that requires selection among competing sources of information in working memory to guide a response". Consistent with the view that selection processes may operate over many types of information, Poldrack et al. (1999) found

that dorsal posterior regions of the LIFG—including the peak activations reported by Thompson-Schill et al.—were associated with not only semantic processing, but also phonological and lexical processing. If it is the case that the LIFG is involved in selecting among competing alternatives across a range of linguistic and non-linguistic domains, this may account for the differences in activation we observe for inflected nouns and verbs. Most verbs are associated with a number of different possible inflections [-ing, -ed, -s] whereas nouns can only be inflected with a plural marker. If recognising a verb stem involves the activation of its inflectional paradigm, then additional LIFG activation may reflect processes of selection amongst the set of inflections that are activated when a verb stem is processed.

An alternate possibility, and one which is more consistent with other recent work on morphological processing, is that the additional activation in the LIFG for inflected verbs compared to inflected nouns reflects morpho-syntactic processing which segments a complex word into its component morphemes. In a related study using spoken inflected words we have shown that these processes preferentially engage the LIFG (Tyler, Stamatakis, Post, Randall, & Marslen-Wilson, 2003b). Subjects heard pairs of regularly [e.g., *jumped-jump*] or irregularly inflected past tense forms [e.g., *thought-think*] and we found more activation in the LIFG for the regularly inflected verbs compared to the irregularly inflected words. We attributed this difference to processes which segment a regularly inflected form into its component morphemes [*jump + ed*] in order to assign different morphemes to their appropriate functions. This same process does not operate on irregularly inflected words since they have no overt morphological structure. There is considerable overlap in the region of LIFG which is activated by inflected verbs in the current study and regularly inflected past tense forms in the Tyler et al. (2003b) study. In the present study the LIFG activation is maximal in BA 44, 45, 47. The anterior to posterior extent encompassed the posterior portion of the inferior frontal gyrus and the activation extended from BA 44/45 to BA 47. In our other study the significant LIFG cluster, centred on BA 44 and extended anteriorly to BA 45. Thus, we suggest that the additional activation for inflected verbs in LIFG in the current experiment reflects processes sensitive to the morphological structure of verbs.⁵ The question we now turn to is why inflected verbs engage the LIFG to a greater extent than inflected nouns since both involve processes of regular morphology. One possibility is that the greater LIFG activation we see for inflected verbs reflects

its role in assigning the different elements of verb morphology to their appropriate structural roles. Verb and noun inflections play different roles in language processing; regular verb inflections mark tense and play an important relational role in developing the structural interpretation of a sentence whereas noun plurals have a primarily semantic role in sentence interpretation. These additional relational aspects of verb inflection may contribute to the greater activation of the LIFG.

This proposal is broadly related to other claims about the neural processing of inflected verbs. For example, Pinker, Ullman et al. have claimed that grammatical and morphological processing are subserved by a procedural memory system which is rooted in the L inferior frontal cortex and subcortical structures such as the basal ganglia (Pinker & Ullman, 2003; Ullman, 2001; Ullman et al., 1997). This system is preferentially engaged in the processing of regularly inflected forms, although the evidence to date has focussed solely on the regular/irregular distinction in verbal morphology.

We are not claiming that the LIFG is only engaged in morphological processes. This is a region that is activated in many studies, both of language processing and cognition more generally, and its function is a matter of intense debate, revolving around the general issue of whether there is evidence for either content- or process-specificity (Demb et al., 1995; Duncan & Owen, 2000; Gabrieli, Poldrack, & Desmond, 1998) or indeed whether the LIFG consists of functional subdivisions which correspond to distinct components of cognitive processes (for example, memory encoding and retrieval (Badgaiyan, Schacter, & Alpert, 2002; Fletcher, Shallice, & Dolan, 2000; Wagner et al., 2001), segmentation in speech and orthographic to phonological conversion in reading (Burton, 2001)). Since our study was not designed to address the extent to which the LIFG subserves a diverse range of cognitive operations (for a discussion see Duncan & Owen, 2000), we remain neutral on this issue.

The overlap in the LIFG between the verb activation in the imaging study and the common lesion in patients who have problems with inflected verbs provides further evidence that the LIFG plays a significant role in processing verb structure. We have argued elsewhere that the LIFG is engaged in processes which decompose regularly inflected past tense words into their component morphemes (Tyler et al., 2002b). The present study extends this previous work by showing that these processes generalise to other types of regular verb morphology apart from the past tense morpheme, and that inflected nouns do not engage this system to the same extent. This may, in turn, relate to the fact that patients with LIFG damage often have syntactic deficits and verbal inflectional morphology plays a syntactic role in sentence comprehension.

Finally, the patients whose lesions we have discussed in this paper show a consistent pattern of behavioural data in a variety of experiments exploring their ability to process various aspects of verbs. Taken together, these studies show that

⁵ Although the present study used written words, there is evidence both from experimental psycholinguistic studies and neuroimaging studies that processing written words involves the activation of a phonological representation. Lukatela, Eaton, Lee, Carello, and Turvey (2002), for example, have reported a series of priming studies which show that, at very early stages of visual word recognition, written words activate a phonological representation. Neuroimaging studies likewise show common neural regions activated for phonological and orthographic processing (Rumsey et al., 1997; Tan, Feng, Fox, & Gao, 2001).

these patients have difficulty in processing inflected verbs but that they can both identify verb stems and access their semantics without any apparent difficulty, suggesting that they do not have a representational deficit for verb stems (Longworth et al., 2002) and instead their problems with verbs actually arise from a disorder with verb morphology. To the extent that these patients can be considered to be typical of patients with perisylvian damage involving the LIFG, then this account may help to explain the nature of supposed verb deficits in such patients.

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