

Temporal and frontal systems in speech comprehension: An fMRI study of past tense processing

Lorraine K. Tyler^{a,b,*}, Emmanuel A. Stamatakis^a, Brechtje Post^a,
Billi Randall^a, William Marslen-Wilson^c

^a Department of Experimental Psychology, University of Cambridge, Downing Street, Cambridge CB 3EB, UK

^b Wolfson Brain Imaging Center, University of Cambridge, Downing Street, Cambridge CB 3EB, UK

^c MRC Cognition and Brain Sciences Unit, Cambridge, UK

Received 8 April 2004; received in revised form 15 February 2005

Available online 18 April 2005

Abstract

A prominent issue in cognitive neuroscience is whether language function is instantiated in the brain as a single undifferentiated process, or whether regions of relative specialisation can be demonstrated. The contrast between regular and irregular English verb inflection has been pivotal to this debate. Behavioural dissociations related to different lesion sites in brain-damaged patients suggest that processing regular and irregular past tenses involves different neural systems. Using event-related fMRI in a group of unimpaired young adults, we contrast processing of spoken regular and irregular past tense forms in a same–different judgement task, shown in earlier research with patients to engage left hemisphere language systems. An extensive fronto-temporal network, linking anterior cingulate (ACC), left inferior frontal cortex (LIFC) and bilateral superior temporal gyrus (STG), was preferentially activated for regularly inflected forms. Access to meaning from speech is supported by temporal cortex, but additional processing is required for forms that end in regular inflections, which differentially engage LIFC processes that support morpho-phonological segmentation and grammatical analysis.

© 2005 Elsevier Ltd. All rights reserved.

Keywords: fMRI; Speech processing; Fronto-temporal network

1. Introduction

A key issue in cognitive neuroscience is the functional and neural architecture of the systems underlying human language, and whether the organisation of these systems should be characterised in terms of a uniform computational and neural process, or whether multiple and distinct underlying mechanisms are involved (Marslen-Wilson & Tyler, 1997; McClelland & Patterson, 2002; Pinker & Ullman, 2002). A particular empirical focus for this issue has been the regular and irregular forms of the English past tense, which contrast sharply in the demands that they make on processes of language learning, comprehension and production. The regular past tense, formed by adding the regular affix /-d/ to the verb

stem (as in *jump-jumped*; *agree-agreed*), is the classic example of a predictable, rule-like process. The irregular past tense, applying to a closed set of about 160 English verbs, represents the converse case of an unpredictable and idiosyncratic process (as in *think-thought*; *make-made*), requiring rote learning of each member of the set. The critical scientific issue raised by these contrasts is whether performance on regular and irregular forms can be accommodated within a single uniform system, as proposed by various connectionist accounts (Joanisse & Seidenberg, 1999; McClelland & Patterson, 2002) or whether separate and specialised processes are required to handle the regular past tense (Marslen-Wilson & Tyler, 1997, 1998; Pinker, 1991, 1999).

This debate has taken a strongly neuropsychological turn over the past five years, with several results (Miozzo, 2003; Tyler et al., 2002a; Ullman et al., 1997) pointing to a dissociation of the underlying neural systems required for the

* Corresponding author: Tel.: +44 1223 766457; fax: +44 1223 766452.
E-mail address: lktyler@csl.psychol.cam.ac.uk (L.K. Tyler).

production and perception of English regular and irregular inflected forms. Patients who typically have damage involving the anterior inferior temporal lobe tend to show poorer performance on the irregulars compared to the regulars in elicitation and reading tasks, while deficits for the regulars are associated with damage to L inferior frontal cortex (LIFC) and underlying structures (Marslen-Wilson & Tyler, 1997, 1998; Patterson, Lambon Ralph, Hodges, & McClelland, 2001; Tyler et al., 2002a; Ullman et al., 1997). This has been shown in a variety of neuropsychological studies probing the comprehension and production of the regular and irregular past tense (Longworth, Marslen-Wilson, Randall, & Tyler, in press; Marslen-Wilson & Tyler, 1997; Tyler et al., 2002a; Ullman et al., 1997).

Focusing here on comprehension rather than production, these neuropsychological dissociations have led us to propose a modified account which moves away from the regularity/irregularity distinction per se, and focuses instead on the role of morpho-phonological parsing processes which allow the segmentation and identification of stems and affixes (Marslen-Wilson & Tyler, 1998, 2003; Tyler, Randall, & Marslen-Wilson, 2002). These processes, associated with LIFC, are required for the analysis of regularly inflected forms in English, with their stem + affix structure, but do not apply to English irregular past tense forms. These have no overt morpho-phonological structure and must be accessed as whole forms. On this account, deficits for the regulars arise when there is disruption of morpho-phonological parsing, associated with damage to the LIFC, whereas deficits for the irregulars reflect damage to temporal lobe structures supporting access from phonological input to representations of stored lexical form.

These proposals can be linked more generally to widely held views about the overall neural and functional architecture of the human language system, almost all of which have in common an emphasis on language-relevant processing structures in superior temporal and inferior frontal areas, and their linkage into a fronto-temporal network. These accounts have begun to be restated in an anatomically and neurophysiologically more explicit framework, deriving from work on the primate auditory system (e.g., Rauschecker & Tian, 2000), and importing notions of a “dorsal/ventral” distinction as already established for primate vision. A number of proposals have begun to emerge for the interpretation of human speech and language systems in this general framework (e.g., Hickok & Poeppel, 2000; Scott & Johnsrude, 2003). These have in common the assumption that ventral pathways in the left temporal lobe are involved in the mapping from phonology onto semantics, but offer divergent views of the nature and function of the dorsal pathways.

In recent publications (Tyler et al., 2002a,b) we have proposed a possible relationship between the global dorsal/ventral distinction and the evidence for processing and neurological dissociations involving the English regular and irregular past tenses based on data from language-impaired patients. The ventral system, on this account, involves tem-

poral lobe structures that mediate access (both phonological and orthographic) to stored lexical representations. We assume these representations are primarily of noun and verb stems, and that regular inflected forms (in contrast to irregular, unpredictable forms) do not have stored access representations associated with them. The dorsal pathway, primarily via the arcuate fasciculus, connects to systems in L inferior frontal areas that are important for the analysis and production of complex morpho-phonological sequences. The language-specific properties of the English past tense would therefore map differentially onto these two systems, with irregular forms handled primarily by temporal lobe systems optimised for access via stored whole forms, while regular forms require in addition the involvement of frontal systems supporting processes of phonological assembly and disassembly. It is likely, furthermore, that these two systems differ in their laterality, with whole word access being supported bilaterally, but with complex forms depending on links to left frontal systems, since homologous right frontal systems do not have the same language-specific functions.

The purpose of the research reported here is to take forward this emerging account of the human speech and language system, using event related fMRI in the intact brain to investigate more directly the neural systems underlying the processing of spoken forms with and without regular inflectional endings—a contrast that in English coincides with the distinction between the regular and the irregular past tense. To do this we use a same–different judgement task whose sensitivity to critical inflectional variables was previously demonstrated in research on patients with LIFC damage (Tyler et al., 2002b). In this task, the patients heard pairs of words and made a decision as to whether they were the same or different. The pattern of performance shown by these patients indicated that the processing of stimulus pairs containing regular past tense inflections depended on brain regions that were damaged in this patient population. By running the same task on normal participants in an fMRI study, we expect to activate the full range of neural regions engaged in the processing of morpho-phonologically complex forms in the intact system, as well as illuminating their relationship to the language system as a whole.

1.1. Phonological cues to morphological complexity

There were two important aspects to the results of the previous same–different study on patients with impairments involving regular morphological morphology (Tyler et al., 2002b). The first was that the performance of the patients was most impaired for real regular pairs (such as *played/play*), compared to a range of phonologically matched conditions, including real-word pseudo-regulars (such as *trade/tray*) and non-word pseudo-regulars (such as *snade/snay*), as well as to irregular pairs (such as *taught/teach*) and to a variety of control conditions. We expect this to be reflected in the current experiment by a distinctive pattern of activation for similar real regular pairs.

These predictions need to be tempered, however, by the second main result of the experiment, which was that the patients were relatively impaired for *all* conditions that contained a potential regular inflectional affix. Thus, although performance was poorest for the real regulars (mean RT of 1420 ms and error rate of 31%), it was also poor for the pseudo-regulars (RT of 1252 ms and error rate of 25%) and for the non-word regulars (mean RT of 1244 ms and error rate of 22%). Performance was much less impaired, and closer to normal levels of accuracy, for control pairs such as *shelf/shell* (RT of 1044 ms and error rate of 5%), where the first member of the pair did not end in a potential inflectional affix.

We interpret this similarity between the three regular past tense conditions (real, pseudo, non-word) as reflecting their common morpho-phonological properties—i.e., that they all share specific phonological features that are diagnostic of the presence of a potential inflectional suffix, and therefore will place specific demands on the neural and functional machinery underlying the perceptual processing of spoken words in English. These diagnostic phonological features have two components: the presence of a word-final coronal consonant (typically /d, t, s, z/) and the agreement in voice between the final coronal consonant and the segment that precedes it.

The sequence ‘passed’ [pa:st] is a potential combination of a verbal stem ‘pass’ [pa:s] with an inflectional suffix, because it ends with the unvoiced coronal consonant /t/, and this agrees in voice with the preceding unvoiced segment /s/. The same applies to the pseudo-regular word ‘cast’, which is potentially analyzable as the (non-existent) verb stem [ka:s], plus the inflectional morpheme /t/, as well as to the non-word sequence ‘nast’, also potentially analysable as [na:s] plus [t]. The control pairs like *shelf/shell*, in contrast, do not observe these diagnostic features. They end in non-coronal consonants, do not agree in voice, and are therefore not *prima facie* candidates for re-analysis as complex forms.

The presence or absence of these diagnostic features should lead a spoken lexical input to interact differentially with the machinery of lexical access and linguistic interpretation. When an input such as [pa:st] is encountered, corresponding to the past tense form ‘passed’, the system needs both to access the semantic and syntactic properties associated with the stem {pass} and to extract the processing implications of the presence of the grammatical morpheme {-t}. We suggest that it is the capacity to support this segmentation that is disrupted in the patients with damage to LIFC, leading to the across-the-board problems for regular inflected forms described above (cf. Tyler et al., 2002b).

In the current experiment, imaging the intact brain, we expect to see a common pattern of increased activation of the proposed left fronto-temporal network across all items with regular inflectional properties, whether they are real word regulars such as *blessed-bless*, real word pseudo-regular pairs like *crest-crest*, or non-word regular pairs like *pleased-pleas*. These are contrasted with irregular past tenses such as *teach/taught*, pseudo-irregular real word pairs like *peach/port* and non-word pairs like *heach/hort*.

A further critical contrast is provided by the same type of control as in the earlier same-different study (Tyler et al., 2002b), with pairs like *shelf/shell* and *claim/clay*. These ‘additional phoneme’ pairs differ by a single final phoneme, like the regulars and the pseudo-regulars, except that here the additional phoneme cannot be interpreted as an inflectional ending, either because it is not a coronal consonant (as in *claim*), or because it is both non-coronal and does not agree in voice (as in *shelf*). These items allow us to evaluate the possibility that any additional processing triggered by forms ending in regular inflections is due to non-morphophonological factors—either the phonological complexity of the structures involved or general requirements for segmentation. A number of earlier results suggest that LIFC may be engaged by tasks requiring overt segmentation (Blumstein, Baker, & Goodglass, 1977; Burton, Small, & Blumstein, 2000). Burton et al. (2000) found LIFC activation when listeners are required to segment words into smaller components in order to make an onset phoneme discrimination (judging whether pairs like *dip/ten* began with the same phoneme). If LIFC functions tapped into by the presence of regular past tenses involve processes specific to morpho-phonological parsing, then we should see less LIFC activation for the additional phoneme pairs, which should not engage these processes.

1.2. Overview

The current experiment is designed to probe the neural systems that are invoked by English regular inflectional morphology in the intact brain. Based on parallel experiments with left frontal patients, we predict that any spoken input which terminates with the phonological pattern diagnostic of a potential inflectional morpheme will not only activate bilateral temporal systems generally involved in the mapping of sound onto meaning, but also areas in left inferior frontal cortex implicated in morpho-phonological segmentation and the processing of grammatical morphemes. Real regular past tense forms, because they do contain these inflectional morphemes, are likely to activate LIFC in a distinctive manner, over and above these general effects. Stimuli which do not share the diagnostic phonological properties, such as irregular past tenses and the monomorphemic additional phoneme pairs, should be less effective in activating these left frontal systems.

2. Method

2.1. Subjects

Eighteen subjects took part in the experiment (nine males, nine females). They were right-handed native speakers of English, with a mean age of 24 years (S.D. 7), and no known hearing deficits. Each gave informed consent and was paid for their participation.

Table 1
The experimental conditions

	Regulars	Irregulars	Additional phoneme
Real			
Different	Stayed–stay	Taught–teach	–
Same	Played–played	Bought–bought	–
Pseudo			
Different	Jade–jay	Port–peach	Pike–pie
Same	Trade–trade	Short–short	Pile–pile
Non-word			
Different	Kay–kayed	Hort–heach	Jike–jie
Same	Tade–tade	Drort–drort	Jile–jile
Baseline			
Different	Pink noise–white noise or white noise–pink noise		
Same	White noise–white noise or pink noise–pink noise		

2.2. Materials and design

We used the phonological similarity judgement task developed for our previous study with patients (Tyler et al., 2002b). Participants heard sets of spoken word-pairs where the first word in the pair was recorded by a male speaker and the second by a female speaker. The task was to judge whether the two words in the pair were the same or different.

There were eight test conditions, as shown in Table 1, with 56 word-pairs in each condition. The first condition (Real) consisted of pairs of regularly inflected words (e.g., *played-play*) and irregularly inflected words (e.g., *taught-teach*). Performance on same/same and same/different regular and irregular pairs was compared with two parallel sets also contrasting in the presence or absence of a potential regular inflectional ending. Pseudo-regular real word (e.g., *crest-crest*) and non-word pairs (*pleased-pless*) were matched to real word regulars (*blessed-bless*), and all ended with a coronal consonant ([d] or [t]) that agreed in voice with the preceding segment. Similarly, pseudo-irregular real word (e.g., *peach/port*) and non-word pairs (e.g., *heach/hort*) were matched to the irregular past tense pairs. The final type of lexical stimulus, the additional phoneme pairs, included both real word (e.g., *claim/clay*) and matched non-word pairs (e.g., *vaim/vay*). The additional phoneme in these pairs, because it was never a coronal consonant, could not be interpreted as a potential inflectional morpheme, unlike the added phoneme in the real regular and pseudo-regular forms.

All real-word stimuli were monosyllabic words matched on syllable structure, familiarity, and lemma and word-form frequencies. All these stimuli, except in the real past tense conditions, were monomorphemic. There were equal numbers of same and different pairs in each condition. The mean duration of the stimuli did not vary across conditions ($F(5, 330) = 1.48$; $p = 0.194$). The stimuli were recorded on DAT-tape in a sound-proofed room and digitised at 16 kHz. The first word in each pair was spoken by a male speaker and the second word was spoken by a female.

The imaging baseline condition consisted of two types of acoustic stimuli – pink and white noise – generated from

the test items using PRAAT software (Boersma & Weenink, 1996). Pink noise is created from frequencies that are used in speech, while white noise is created from a broader range of frequencies. By generating the baseline items from the test stimuli we ensured that their duration and prosodic envelope was identical across test and baseline conditions. Just as in the test conditions, there were equal numbers of same and different pairs. The choice of baseline task and stimuli was intended to present listeners with an auditory discrimination task that made similar demands to the test materials but without triggering activation of speech and language processing areas in the brain.

2.3. Procedure

We used a sparse imaging technique (Hall et al., 1999) so that subjects could hear the auditory stimuli without interference from scanner noise. During each 7 s event, while the scanner remained silent, two sets of word-pairs from the same experimental condition were presented sequentially, with a 100 ms interval between the two words of a pair and a 2 s interval between each pair. The first trial in the event was preceded by a period of silence varying from 450 to 1250 ms (in 200 ms steps) to ensure jittering of the first trial across events. Jittering of the second trial automatically resulted from the varying duration of the words in the first trial. Presentation and timing of the stimuli was controlled by the DMDX experimental software package (Forster & Forster, 1990). Each 7 s event was followed by a 3 s period of scanner activity, giving a total trial length of 10 s.

The events were pseudo-randomly organised into three sessions of 84 events, with equal numbers of items from each condition within each session. The order of sessions was varied across subjects. Subjects heard stimulus pairs and used the index and middle fingers of their right hand to indicate whether the two stimuli were the same or different.

2.4. MRI acquisition and imaging analysis

Scanning was carried out on a 3 T Bruker Medspec Avance S300 system at Wolfson Brain Imaging Center, Cambridge, UK, using a gradient-echo EPI sequence (TR = 10 s, TE = 27 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, 86 repetitions) with head coils, 200 kHz bandwidth and spin echo guided reconstruction. T1-weighted scans were acquired for anatomical localisation.

Imaging data analysis was performed using SPM99 software (Wellcome Institute of Cognitive Neurology, www.fil.ion.ucl.ac.uk), implemented in Matlab (Mathworks Inc., Sherborn, MA, USA). Initial pre-processing consisted of image realignment to account for head motion. An undistortion procedure corrected for EPI distortions due to magnetic field inhomogeneities (Cusack, Brett, & Osswald, 2003; Jezzard & Clare, 1999). The images were 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, except in areas of low BOLD signal (caused by susceptibility artefacts) where 12 parameter linear affine transformations were used. These areas were defined by mask images constructed by experienced observers. The spatially normalised images were smoothed with an isotropic 12 mm full-width half-maximal Gaussian kernel. The data for each subject were modelled using the general linear model (Friston et al., 1995). Three sessions and nine event types were entered into the model. The BOLD response was modelled as a box car response, not convolved with HRF, with one scan per epoch, and scaling was applied to a grand mean of 100 over all voxels and scans within each session. Additionally for each session we included six confounding covariates (translations and rotations in x , y and z directions produced at the realignment stage) to capture residual movement related artefacts. Contrast images from each subject were combined into a group random effects analysis.

Activations 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. Given that regular past tense deficits are associated with damage to the L perisylvian regions, we carried out two planned region of interest (ROI) analyses on these areas, one focussing on the LIFC and the other on the L temporal cortex, using the small volume correction (SVC) technique. SVC makes a formal assessment of the new search volume and calculates corrected p values based on this (Worsley et al., 1996). The LIFC and L temporal cortex regions were introduced to the analyses in the form of mask (B&W) images, constructed from the Talairach and Tournoux atlas of the human brain, by outlining the regions on the atlas and transforming the outlines to a digital image. SPM coordinates are given in Montreal Neurological Institute (MNI) space, and these are reported in the Tables. Regions were identified by converting the coordinates to Talairach space with a nonlinear transformation (Brett, 2001).

3. Results

3.1. Behavioural data

Behavioural data collected during scanning were consistent with the results for the normal controls in our earlier study (Tyler et al., 2002b). Overall RTs (1099 ms) to the regular sets (real regulars, pseudo-regulars, and non-word regulars) were slower than to the irregulars (992 ms), with $F(1, 330) = 55.7$; $p < 0.001$. The additional phoneme conditions (mean RT: 1055 ms) were intermediate, being faster than the regular conditions (Scheffe test: $p < 0.025$) but slower than the irregular conditions (Scheffe test: $p = 0.001$). This pattern mainly reflects intrinsic differences in the point at which different forms diverge from their stems, and thus the earliest point at which the same/different decision could be made. For the irregulars, the past tense form (e.g., *slept*) typically

diverges from its stem (*sleep*) earlier in the word (during the vowel) than for the regulars, whereas a past tense form (e.g., *played*) only diverges unequivocally from its stem (*play*) at the final phoneme (and similarly for additional phoneme pairs such as *claim/clay*).

Although these differences in the timing of relevant information led to faster response times for the irregulars, there were no significant differences in error rates between the regulars (5.1%) and the irregulars (4.3%) ($F < 1$), suggesting that the two types of item nonetheless did not differ saliently in terms of overall difficulty in making the same/different judgement. Overall error-rates were higher in the additional phoneme conditions (7.2%), differing significantly from the irregulars (Scheffe test: $p < 0.025$) but not from the regulars (Scheffe test: $p > 0.4$).

Looking at the subsets of regular and irregular materials, RTs and errors did not differ across the real, pseudo and non word past tense conditions (RTs: $F_2(2, 330) = 2.03$; $p > 0.1$; errors: ($F_2(2, 330) = 1.28$; $p > 0.2$), nor was there any interaction with type of past tense (RTs: $F_2(1, 330) = 1.43$; $p > 0.2$; errors: ($F_2(2, 330) = 1.63$; $p > 0.1$). The baseline conditions (pink noise/white noise comparisons) generated many more errors (15.4%) compared to the speech conditions (5.3%; $t[502] = 7.55$, $p < 0.001$), suggesting that the discrimination task was more difficult for the baseline items.

3.2. Imaging data

The first step in the imaging analysis was to determine whether the task activated those neural regions typically engaged in spoken language processing. We addressed this question by contrasting the activation for speech (words and non-words) against the baseline. As Fig. 1 shows, spoken language primarily activated the superior temporal gyrus including Heschl's gyrus (HG) in both hemispheres, consistent with other studies (e.g., Binder et al., 2000). In the LH this activation extended posteriorly and inferiorly from HG and included the middle temporal gyrus (MTG) and laterally and anteriorly into the tip of BA22 (see also Davis & Johnsrude, 2003).

The first focus of the subsequent analyses was the overall contrast between regulars and irregulars. In analyses that included the real and pseudo-past forms of the regulars and irregulars, as well as their non-word counterparts, we found a robust pattern of differences, distributed across two main regions (see Table 2 and Fig. 2a), and implicating a fronto-temporal network of activations. The overall regular/irregular comparison produced a significant cluster of activation in left superior temporal gyrus (STG) including Heschl's gyrus (BA41). This cluster extended posteriorly and laterally to include BA42 and BA22 and anteriorly to include BA21 and BA22. A small part of the left middle temporal gyrus (MTG) in BA21 was also included. A second significant cluster was located at the RSTG and included a smaller part of Heschl's gyrus (BA41) than the LSTG cluster. This cluster included most of the anterior and lateral aspect of the RSTG BA21 and

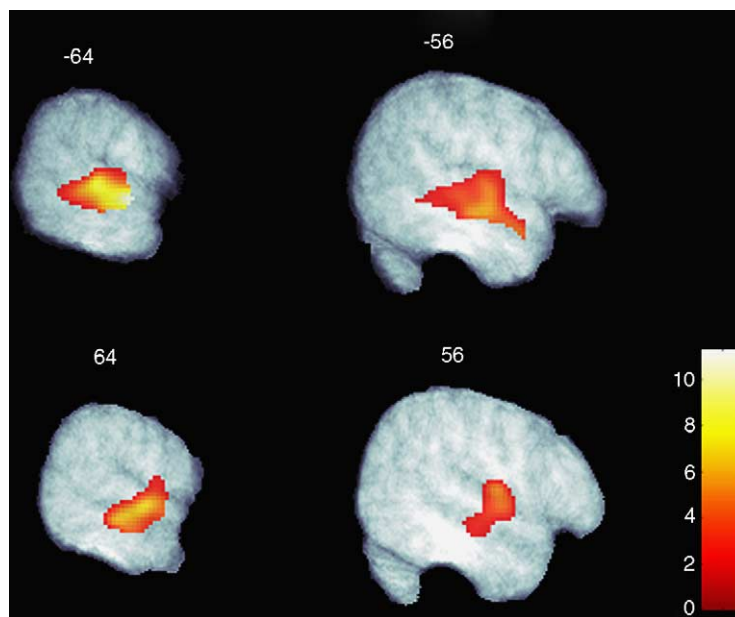


Fig. 1. Significant activations for the contrast of speech minus baseline were found primarily in the STG including HG in both hemispheres. In the LH the activation included the MTG. The activations are shown superimposed on the mean T1 image of the 18 volunteers. Talairach x values are shown above each panel. The colour bar indicates the range of T values for the activations shown.

22 and extended posteriorly to BA42. A third smaller cluster was activated in the left inferior parietal lobule (LIPL) (BA40). Following SVC a cluster in the LIFC also became significant. This centred on BA44 and extended inferiorly into BA45.

There were no areas that were significantly more active for the irregulars compared to the regulars, even at a lower threshold.

Examining the real regulars and the real irregulars on their own, we see a similar pattern of activation, with an additional peak in the anterior cingulate (see Table 3 and Fig. 2b). There is again significant activation in the LSTG, with a peak at the border of the STG and Heschl's gyrus, and extending laterally and anteriorly into BA41 and BA42 and including BA21 in the left middle temporal gyrus (MTG). A second cluster in RSTG (BA22) included Heschl's gyrus (BA41) and regions both posterior and anterior to it, extending inferiorly

into MTG (BA21/22). There was also significant activation in the L anterior cingulate (LAC) which extended into the RH. Additionally, in a ROI analysis using the small volume correction (SVC), we found a significant cluster in the LIFC, centring on the pars opercularis (BA44). At a lower threshold ($p < 0.01$) this extended anteriorly into the pars triangularis (BA45; see Fig. 3).

The stronger activation for the real regulars versus the real irregulars in the anterior cingulate is reflected in an interaction between past tense type (regulars/irregulars) and word type (real past/pseudo past). This produced a significant cluster in the ACC bilaterally, focused in BA32, with a strong LACC peak at $-6, 16, 34$, and a linked RACC peak at $4, 21, 30$. There is significantly greater activation for the regulars compared to the irregulars, but only for the real word past tense forms and not for the pseudo forms. This means that there are differential effects of regularity in the ACC which depend on the lexical

Table 2
Significant activations for the contrast all regulars minus all irregulars

Regions	Cluster level		Voxel level		Coordinates		
	$P_{\text{corrected}}$	Extent	$P_{\text{corrected}}$	Z	x	y	z
LSTG (BA42)	0.000	1414	0.006	5.20	-46	-26	8
LSTG (BA42)			0.010	5.07	-56	-24	10
LMTG (BA21)			0.610	3.77	-56	-48	8
RSTG (BA22)	0.000	834	0.012	5.03	58	-14	2
RSTG (BA22)			0.210	4.22	58	-28	4
RSTG (BA22)			0.246	4.16	62	-6	10
R Inf. par. lobule (BA40)	0.028	252	0.266	4.14	46	-42	34
R Inf. par. lobule (BA40)			0.603	3.78	38	-44	42
LIFC (BA44) ^a pars opercularis	0.001	112	0.005	4.36	-50	12	20

^a After SVC.

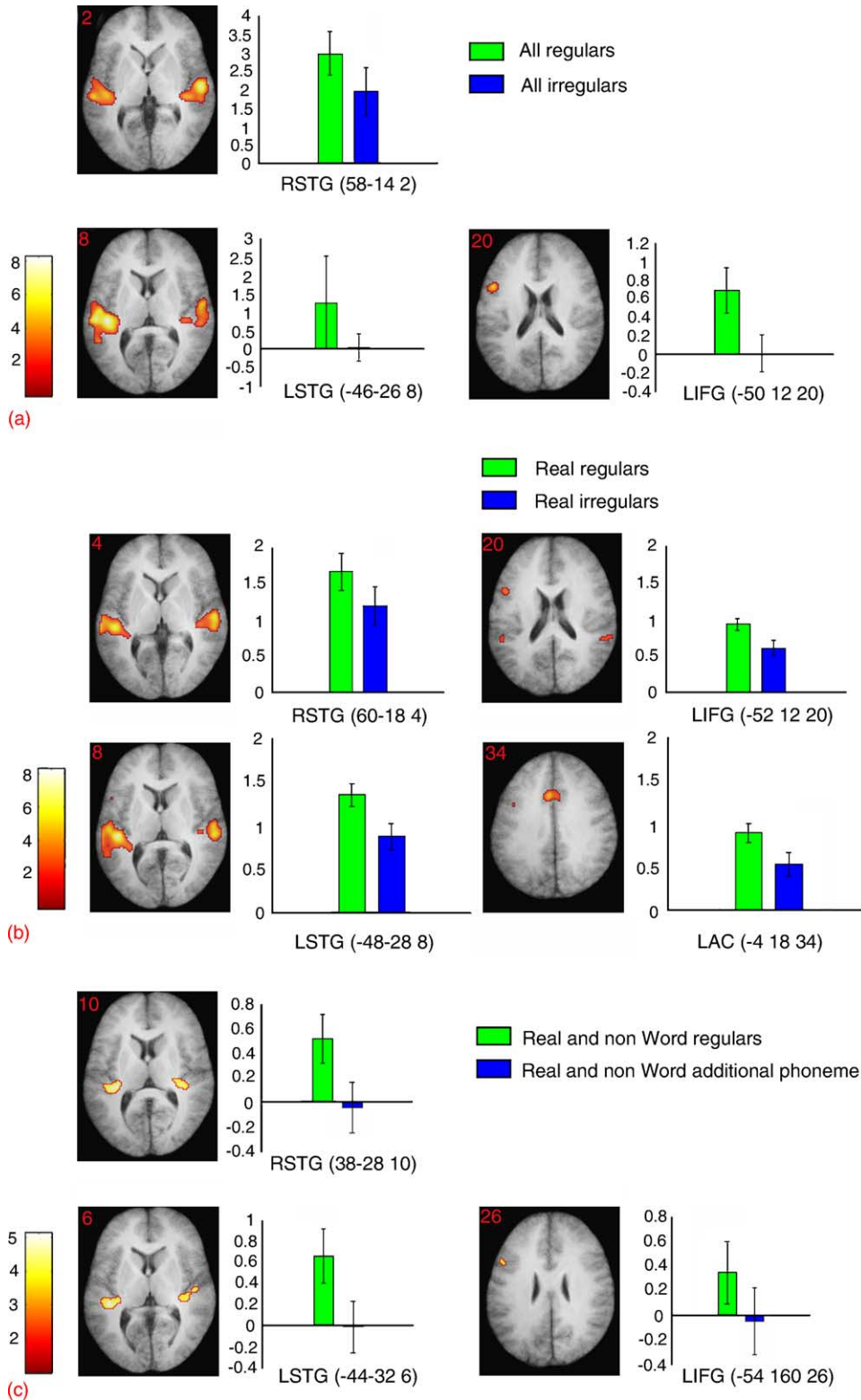


Fig. 2. Significant activations shown for a range of contrasts. The colour bars indicate the range of *T* values for each activation. The plots show effect size in arbitrary units. We use the neurological convention (i.e., right-hand side of the image corresponds to right hemisphere). The activations are superimposed on the mean T1 image of the 18 volunteers. (a) Significant activations for the overall contrast of regulars (real, pseudo, non-word) minus irregulars (real, pseudo, non-word). Significant clusters were found in the RSTG, LSTG, and LIFC. Activation peaks are displayed in parentheses. (b) Significant activations for the contrast of real regulars minus real irregulars. Significant clusters were found in the RSTG, LSTG, LACC, and LIFC. Activation peaks are displayed in parentheses. (c) Significant activations for the contrast of regulars (real, non-word) vs. additional phoneme (real, non-word). Significant clusters were found in the RSTG, LSTG, and LIFC.

Table 3
Significant activations for the contrast real regulars minus real irregulars

Regions	Cluster level		Voxel level		Coordinates		
	$P_{\text{corrected}}$	Extent	$P_{\text{corrected}}$	Z	x	y	z
L Heschl's gyrus (BA41)	0.000	1337	0.007	5.15	-48	-28	8
L Heschl's gyrus (BA41)			0.196	4.24	-56	-20	10
LMTG (BA22)			0.228	4.19	-66	-30	4
RSTG (BA22)	0.000	918	0.109	4.42	60	-18	4
RSTG (BA42)			0.111	4.42	60	-26	8
RSTG (BA21)			0.186	4.25	46	-28	-4
L cingulate gyrus (BA32)	0.040	225	0.321	4.06	-4	18	34
LIFC (BA44) ^a pars opercularis	0.003	80	0.056	3.60	-52	12	20
LIFC (BA44) ^a pars opercularis			0.105	3.37	-44	8	32

^a After SVC.

and morphological status of the words involved—whether they are genuinely segmentable into a stem and an inflectional affix (as in *played/play*), or only potentially (as in *trade/tray*).

A second interaction reflecting distinctive effects for the real regulars, using the small volume correction (SVC), emerged from the interaction between regulars and irregulars and word type (real words/non-words). This revealed a significant LIFC cluster in BA47, with a peak at -50, 36, -6, and a further cluster in the L temporal lobe (BA22), at -64, -22, 4, which extended posteriorly and inferiorly to the middle temporal gyrus (BA22). The activation in the LIFC extended into BA45 at a lower threshold and at this threshold there was a further cluster of activation in BA44 (Fig. 3). These activations reflected a significant difference in activation levels between regulars and irregulars, but only for the real word contrasts and not for the non-words.

In the third main focus of the analyses, we compared the regulars with the additional phoneme conditions. In both these conditions the word pairs differ by a single phoneme, but in the additional phoneme conditions (such as *claim/clay*) this phoneme is not a potential grammatical morpheme. The comparison between the regulars and the additional phoneme conditions produces a similar pattern to the contrast between the regulars and the irregulars, consistent with the view that the important factor here is the potential segmentability of the input into a stem plus inflectional morpheme. This morpho-phonological segmentability is not a feature either of the irregulars or the additional phoneme cases. Indeed, when the irregulars and the additional phoneme conditions are compared in the same way, there is no sign of the left fronto-temporal

pattern seen for comparisons involving the regulars, even at a very low threshold.

As illustrated in Fig. 2c and Table 4, there is significantly greater activation for regulars over additional phonemes in the STG bilaterally. With SVC two additional clusters in the LIFC (BA44, 45) are significant (Fig. 3). Interestingly, these LIFC effects also hold for the regular non-word/additional phoneme non-word contrast, where there is a significant pair of activations (under SVC) in the LIFC at -50, 36, 6 and -48, 36, -8, but there are no longer significant differences in left or right temporal lobes. Since neither pair has any lexical content, being non-words with non-word stems, they will not strongly activate potential lexical candidates for further analysis. The regular non-words, nonetheless, retain the diagnostic inflectional ending, which we argue triggers morpho-phonological segmentation processes in the LIFC, as reflected in the activations seen in these regions.

There were no significant effects or interactions in the reverse contrast, nor, as mentioned above, in comparisons between the irregulars and the additional phoneme conditions. These results suggest that it is the morpho-phonological structure (real or potential) of the regular stimuli that produces additional activation in STG and LIFC, and not a more general comparison process – possibly involving overt segmentation (cf. Burton et al., 2000) – induced by the similarity of the two members of the same/different pair.

The pattern of results for the regular/irregular/additional phoneme contrasts allows us to address possible concerns about “time-on-task” effects contributing to the different patterns of activation for regulars and irregulars. Overall RTs for

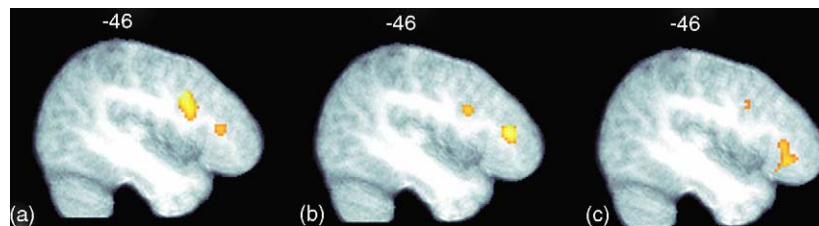


Fig. 3. Significant activations in two regions of the LIFC for the contrasts of (a) regulars minus irregulars, (b) regulars minus additional phoneme and (c) the interaction of regular/irregular and word/non-word. The activations are located in both pars opercularis and pars triangularis and are shown superimposed on the mean T1 image of the 18 volunteers on Talairach $x = -46$ (Fig. 2a).

Table 4
Significant activations for the contrast regulars minus additional phonemes

Regions	Cluster level		Voxel level		Coordinates		
	$P_{\text{corrected}}$	Extent	$P_{\text{corrected}}$	Z	x	y	z
LSTG (BA22)	0.007	321	0.420	3.99	−44	−32	6
L Heschl's gyrus (BA41)			0.523	3.89	−34	−28	10
LSTG (BA22)			0.884	3.51	−58	−28	2
R Heschl's gyrus (BA41)	0.073	169	0.747	3.68	38	−28	10
LSTG (BA22)			0.814	3.60	50	−16	4
LIFC (BA45) ^a	0.069	11	0.095	3.44	−50	34	8
LIFC (BA44) ^a	0.052	15	0.109	3.39	−54	16	26

^a After SVC.

same–different judgements average 107 ms longer for regulars than irregulars. This is not accompanied by a difference in error rate, and at least in part reflects the timing with which discriminatory information becomes available in the two types of material. It is unlikely, however, that this longer time-on-task could generate the fronto-temporal patterns we observed because we do not see a consistent pattern of increased fronto-temporal activation associated with condition-related differences in RT. In particular, there is no sign of either LIFC or STG activation for the additional phoneme/irregular contrast, where additional phoneme RTs are 63 ms slower compared to the irregulars. Regular RTs, however, which are 44 ms slower than in the additional phoneme condition, do show enhanced fronto-temporal activation.

Finally, we examine in more detail the distribution of effects in the LIFC across the various contrasts examined above. As Fig. 3 suggests, there is a systematic pattern common to the contrasts between regulars and irregulars and between regulars and the additional phoneme conditions, as well as showing up in the interaction between regularity and lexical status (word/non-word). In each case there are two distinct loci of activation, in the pars opercularis and the pars triangularis respectively. This clustering of effects in these two LIFC regions may reflect activations at sites related to different speech processing streams. Studies on humans and macaques suggest that neurons in posterior STS project to regions of superior LIFC which overlap with area BA44, while more inferior regions of the LIFC, overlapping with BA45, receive projections from more anterior STS regions (Scott & Johnsrude, 2003).

In summary, the imaging results show that the set of regular stimuli (real, pseudo, and non-word) engage bilateral STG and regions of the LIFC (the pars opercularis and triangularis) more strongly than both the irregular and the additional phoneme sets. The real regulars elicit an additional activation in bilateral anterior cingulate.

4. Discussion

The data reported here make two main points. First, they confirm, in a neuro-imaging study of the intact brain, that

regular and irregular past tenses in English differentially activate the cortical language system, and that these differences cannot straightforwardly be reduced to lower-level phonological factors. The critical factor seems to be the presence of a potential regular inflectional affix.

Second, the results here make it clear that we are dealing with an extended fronto-temporal network, and that the additional demands made by regular inflected forms extend not only to LIFC structures, but also to the superior temporal cortex, and possibly to mid-line regions in the anterior cingulate. The patterning of these effects is notably consistent with earlier neuropsychological results, suggesting a convergence of constraints on neural structure/function relations from these two sources.

We now turn to a consideration of the possible functional interpretation of this fronto-temporal network, and why processes involving the regular past tense inflection should be differentially affected when the LIFC is damaged. Both neuropsychological and neuroimaging evidence associate superior temporal regions, especially on the left, with the access of lexical form and meaning from the phonological input (Kertesz, Lau, & Polk, 1993). In the neuropsychological literature, the focus has been specifically on the role of the posterior regions of the STG – Wernicke's area – in spoken language comprehension. This region has been claimed to store 'the memory images of speech sounds' (Wernicke, 1874), with connections between Wernicke's area and other cortical regions (temporal and frontal) enabling access to both meaning and speech production (Lichtheim, 1885). In support of the view that this region is specifically involved in the processing of speech, neuroanatomical studies have shown that posterior STG is larger in the left hemisphere, suggesting that it is specialised for speech processing (Geschwind & Levitsky, 1968), and patients with LH damage in this region are claimed to have spoken language comprehension deficits (e.g., Damasio, 1992; Kertesz, 1981).

Neuroimaging studies typically find that speech processing activates broad regions of bilateral STG (Scott, Blank, Rosen, & Wise, 2000). Consistent with this, in the present study we find that speech (both words and non-words) activates the same extensive region of STG, extending both anteriorly and posteriorly from Heschl's gyrus. Within this

region, the regularly inflected sets produce significantly enhanced activation in bilateral STG compared to the irregular sets. In the LH, the greater activation for the regulars compared to the irregulars is centred on Wernicke's area, with a peak activation at $-48, -27, +9$ extending laterally to $x = -65$ and anteriorly to $y = -19$. Essentially the same region is more active for the real word regulars compared to the irregulars in the interaction of regularity and word type (real words and non-words). The peak of the cluster was located at $x = -63, y = -21, z = +5$. This is close to the peak activations reported in other imaging studies which have explored the neural underpinnings of speech processing. For example, Wise et al. (2001) report peak activations in the same region but slightly more posterior, at $-61, -35, +6$, in response to words compared to signal correlated noise. Binder et al. (2000) report mean activations for speech relative to non-speech across a variety of studies in similar regions ($x = -55$ [S.D. 2.3], $y = -20$ [S.D. 10.9], $z = +3$ [S.D. 4.1]).

Although the exact function of the posterior STG in speech processing and spoken language comprehension is unresolved, it is clear that it plays an important role in the mapping of speech inputs onto stored representations of word meaning, and that it is particularly active during the processing of both real regular inflected forms, and of potentially inflected forms. We propose that this reflects the special processing demands made by such forms. Although *jump*, or any other uninflected stem, can map straightforwardly onto lexical representations, the presence of the affix [t], as in the past tense *jumped*, seems to place additional demands on this access process. To interpret *jumped* correctly, and to allow the process of lexical access to proceed normally, the past tense affix needs to be recognised, and assigned to a different linguistic function. This process seems to require an intact LIFC, and intact links to left superior temporal cortex. Note that irregular past tense forms are not subject to the same additional processing requirement. They are assumed to be accessed as whole forms, exploiting the same temporal lobe systems as uninflected stems.

Suggestive evidence for this functional interpretation comes from the priming results recently reported by Longworth et al. (in press), showing that patients with LIFC damage, and difficulties with regular inflectional morphology, show deficits in semantic priming when the primes are regularly inflected forms, as in pairs like *jumped/leap*. At the same time, critically, they show normal performance both for pairs with stems as primes, as in *jump/leap*, and for pairs where the prime is an irregular past tense form, as in *shook/tremble*.

Normal semantic priming performance in these auditory–auditory paired priming tasks requires rapid access to lexical semantic representations in the processing of both prime and target. The patients' preserved performance for stem and irregular spoken primes shows that the systems supporting fast access of meaning from speech are still intact for these types of input. The decrement in performance on the regular inflected forms means that these

inflected forms make special processing demands, and that an intact LIFC is necessary to meet these demands.

The further critical component of our account is that these special processing demands are elicited by any input that shares the diagnostic properties of an inflectional affix, whether or not these forms correspond to existing phonological access representations. Unless the system attempts the morpho-phonological segmentation of forms like *trade* or *snade*, it cannot rule out the possibility either that the pseudo-regular *trade* is actually the real regular *tray* in the past tense, or that *snade* is the past tense of the potentially real stem *snay*. This, we argue, requires obligatory access to left inferior frontal regions. Additional evidence to support the across-the-board impact of the inflectional rhyme ending comes from a recent behavioural study (Post, Marslen-Wilson, Randall, & Tyler, 2004), which not only replicates the finding that real, pseudo and non-word regulars group together against a range of control conditions, but also suggests that similar contrasts apply to English 's' inflections, as in *jumps* or *yards*, which obey the same constraints of coronality and agreement in voice.

Consistent with these claims, our results show that regions of the LIFC – especially the pars opercularis (BA44) and the pars triangularis (BA45) – are more strongly implicated in processing regularly inflected forms (see Fig. 3), even when these are non-words. These regions of the LIFC are associated with the processing of grammatical morphemes, and with syntactic function more generally (Caplan, Alpert, & Waters, 1998; Just, Carpenter, Keller, Eddy, & Thulborn, 1996; Zurif, 1995). Neuropsychological studies associate damage to these regions with both syntactic and morphological deficits (Goodglass, Miceli, & Caramazza, 1988; Marslen-Wilson & Tyler, 1997, 1998; Tyler, 1992), and neuroimaging studies have also reported significant activations in BA44 and 45 for syntactic processing, which overlap with the activations that we find in the current study for the regulars compared to the irregulars (Embick, Marantz, Miyashita, O'Neill, & Sakai, 2000; Friederici, Opitz, & von Cramon, 2000). There is also evidence from a number of sources for the same regions being involved in processes of phonological segmentation (Zatorre, Evans, Meyer, & Gjedde, 1992).

The data suggest that these inferior frontal regions, together with the superior temporal areas discussed previously, are involved in the analysis of forms like *played*, which we propose requires the simultaneous access of the lexical content associated with the stem *play* (primarily mediated by temporal lobe systems), and of the grammatical implications of the {-d} morpheme (primarily mediated by inferior frontal systems). Unless these different components of the word-form are assigned to their appropriate processing destinations, effective on-line processing of such forms is disrupted, as demonstrated in the priming studies mentioned earlier (Longworth et al., in press; Marslen-Wilson & Tyler, 1997; Tyler et al., 2002a). In contrast, for irregular forms like *gave* or *bought*, no such on-line differentiation is either required or possible. Patients with LIFC damage do not have

problems with the irregulars, suggesting that their processing does not necessitate the involvement of this region (Tyler et al., 2002a,b). Access for words like *gave* is mediated, as a whole form, through temporal lobe systems, and does not require segmentation into phonologically separate stem and affix components (Marslen-Wilson & Tyler, 1998). Thus, although irregular past tense forms will activate LIFC to some extent, because of the syntactic implications of their grammatical properties, immediate access to lexical meaning does not obligatorily require LIFC phonological parsing functions in the same way as regular past tense forms.

On this account, the increased activation for regulars (and pseudo-regulars) in temporal and inferior frontal areas reflects, on the one hand, the role of LIFC processes involved in analysing grammatical morphemes, and on the other the continuing STG activity involved in accessing lexical representations from the stems of regular and pseudo-regular inflected forms. The LIFC functions invoked here are likely to support both morpho-phonological parsing, segmenting complex forms into stems and affixes, and syntactic processes triggered by the presence of grammatical morphemes such as the past tense marker.

A final consideration here is the management of the proposed processing relationship between L frontal and temporal regions. Several lines of evidence suggest that the integration of information between superior temporal and L frontal areas may be modulated by anterior midline structures including the anterior cingulate, which both neuroanatomical and functional neuro-imaging evidence suggest is well suited for this role. Work with nonhuman primates shows that the ACC projects to or receives connections from most regions of frontal cortex (Barbas, 1995) and from superior temporal cortex (Pandya, Vanhoesen, & Mesulam, 1981). Recent neuro-imaging data not only implicate the ACC in the modulation of fronto-temporal integration (Fletcher, McKenna, Friston, Frith, & Dolan, 1999), but also show it to be active in situations requiring the monitoring of interactions between different information processing pathways (Braver, Barch, Gray, Molfese, & Snyder, 2001).

On this view, the increased activation of the ACC by regular inflected forms (see Fig. 2b) may reflect the greater demands made on this monitoring function when complex forms such as *jumped* need to be parsed into a stem + affix, with the bare stem then able to act as a well-formed input to STG lexical access processes. Consistent with this, an effective connectivity analysis of the current data, assessing the measured activity in selected brain regions in terms of the extent to which activity in that region predicts activity in other regions (Friston et al., 1997), shows significant dependencies between the key sites, with LIFC regions, in interaction with ACC, modulating activity in a range of left temporal lobe structures (Stamatakis, Marslen-Wilson, Tyler, & Fletcher, 2004). However, given the present experiment alone, we cannot exclude the possibility that these interactions involving the ACC reflect differences in task requirements when regular past tense forms are involved—although

the evidence from error rates suggests that this is not simply because there is a difference in difficulty between regular and irregular same/different pairs.

In summary, we propose that the fronto-temporal neural system involved in language processing is critically involved in the on-line process of separating the speech input into complementary processing streams, on the one hand extracting information about meaning, conveyed by uninflected nouns and verb stems, such as *house* or *stay*, and on the other information about grammatical structure, conveyed in part by inflectional morphemes such as the past tense {-d}. These proposals point to a more specific and dynamic account of how language function is organised in the human brain, and provide a more general functional framework within which to interpret the behavioural and neuropsychological differences in the processing of English regular and irregular past tense forms.

Acknowledgements

We thank Matt Davis and Ingrid Johnsrude at the MRC Cognition and Brain Sciences Unit for helpful comment and discussion at many stages of this project, and the staff at the Wolfson Brain Imaging Centre for help with neuro-imaging. This research was supported by an MRC programme grant to LKT.

References

- Barbas, H. (1995). Anatomic basis of cognitive-emotional interactions in the primate prefrontal cortex. *Neuroscience and Biobehavioural Reviews*, 19(3), 499–510.
- Binder, J. R., Frost, T. A., Hammeke, P. S. F., Bellgowan, P. S. F., Springer, J. A., Kaufman, J. N., et al. (2000). Human temporal lobe activation by speech and nonspeech sounds. *Cerebral Cortex*, 10, 512–528.
- Blumstein, S. E., Baker, E., & Goodglass, H. (1977). Phonological factors in auditory comprehension in aphasia. *Neuropsychologia*, 15, 19–30.
- Braver, T. S., Barch, D. M., Gray, J. R., Molfese, D. L., & Snyder, A. (2001). Anterior cingulate cortex and response conflict: Effects of frequency, inhibition and errors. *Cerebral Cortex*, 11, 825–836.
- Brett, M. (2001). Using the Talairach atlas with the MNI template. *NeuroImage*, 13(6), S85.
- Boersma, P., & Weenink, D. (1996). *Report of the Institute of Phonetic Sciences*, University of Amsterdam, pp. 132 (<http://www.fon.hum.uva.nl/praat/>).
- Burton, M., Small, S., & Blumstein, S. (2000). The role of segmentation in phonological processing: An fMRI Investigation. *Journal of the Cognitive Neuroscience*, 12, 679–690.
- Caplan, D., Alpert, N., & Waters, G. (1998). Effects of syntactic structure and propositional number on patterns of regional cerebral blood flow. *Journal of the Cognitive Neuroscience*, 10, 541–552.
- Cusack, R., Brett, M., & Osswald, K. (2003). Evaluation of the use of magnetic field maps to undistort echo-planar images. *NeuroImage*, 18, 127–142.
- Damasio, A. (1992). Aphasia. *New England Journal of Medicine*, 326, 531–539.
- Davis, M., & Johnsrude, I. (2003). Hierarchical processing in spoken language comprehension. *Journal of Neuroscience*, 23(8), 3423–3431.

- Embick, D., Marantz, A., Miyashita, Y., O'Neill, W., & Sakai, K. (2000). A syntactic specialisation for Broca's area. *Proceeding of the National Academy of Sciences*, 97(11), 6150–6154.
- Fletcher, P., McKenna, J., Friston, K. J., Frith, C., & Dolan, R. J. (1999). Abnormal cingulate modulation of fronto-temporal connectivity in schizophrenia. *NeuroImage*, 9(3), 337–342.
- Forster, K. I., & Forster, J. C. (1990). *The DMASTR display system for mental chronometry*. Tucson, AZ: University of Arizona.
- Friederici, A., Opitz, B., & von Cramon, Y. (2000). Segregating semantic and syntactic aspects of processing in the human brain: An fMRI investigation of different word types. *Cerebral Cortex*, 10, 698–705.
- Friston, K. J., Buechel, C., Fink, G. R., Morris, J., Rolls, E., & Dolan, R. J. (1997). Psychophysiological and modulatory interactions in neuroimaging. *NeuroImage*, 6, 218–229.
- Friston, K. J., Holmes, A., Worsley, K., Poline, J.-B., Frith, C., & Frackowiak, R. (1995). Statistical parametric maps in functional imaging: A general linear approach. *Human Brain Mapping*, 2, 189–210.
- Geschwind, N., & Levitsky, W. (1968). Human brain: Left–right asymmetries in temporal speech region. *Science*, 161, 186–187.
- Goodglass, H., Miceli, G., & Caramazza, A. (1988). Dissociation of inflectional and derivational morphology. *Brain and Language*, 35, 24–65.
- Hall, D., Haggard, M. P., Akeroyd, M. A., Palmer, A. R., Summerfield, A. Q., Elliott, M. R., et al. (1999). Sparse temporal sampling in auditory fMRI. *Brain Mapping*, 7(3), 213–223.
- Hickok, G., & Poeppel, D. (2000). Towards a functional neuroanatomy of speech perception. *Trends in Cognitive Sciences*, 4(4), 131–138.
- Jezzard, P., & Clare, S. (1999). Sources of distortion in functional MRI data. *Human Brain Mapping*, 8, 80–85.
- Joanisse, M., & Seidenberg, M. (1999). Impairments in verb morphology after brain injury. *Proceedings of the National Academy of Sciences*, 96, 7592–7597.
- Just, M., Carpenter, P. A., Keller, T. A., Eddy, W. F., & Thulborn, R. (1996). Brain activation modulated by sentence comprehension. *Science*, 274, 114–116.
- Kertesz, A. (1981). Anatomy of jargon. In J. Brown (Ed.), *Jargonaphasia*. New York: Academic Press.
- Kertesz, A., Lau, W.K., & Polk, M. (1993). The structural determinants of recovery in Wernicke's aphasia. *Brain and Language*, 44, 153–164.
- Lichtheim, L. (1885). Uber aphasia. *Deutsches Archiv für klinische Medizin, Leipzig*, 36, 204–268. [English translation: On aphasia. *Brain (Oxford)*, 7, 433–484].
- Longworth, C. E., Marslen-Wilson, W. D., Randall, B., & Tyler, L. K. (in press). Getting to the meaning of the regular past tense: Evidence from neuropsychology. *Journal of Cognitive Neuroscience*.
- Marslen-Wilson, W. D., & Tyler, L. K. (1997). Dissociating types of mental computation. *Nature*, 387, 592–594.
- Marslen-Wilson, W. D., & Tyler, L. K. (1998). Rules, representations, and the English past tense. *Trends in Cognitive Science*, 2, 428–435.
- Marslen-Wilson, W. D., & Tyler, L. K. (2003). Capturing underlying differentiation in the human language system. *Trends in Cognitive Sciences*, 7(2), 62–63.
- McClelland, J., & Patterson, K. (2002). Rules or connections in past-tense inflections: What does the evidence rule out? *Trends in Cognitive Sciences*, 6(11), 465–472.
- Miozzo, M. (2003). On the processing of regular and irregular forms of verbs and nouns: Evidence from neuropsychology. *Cognition*, 87(2), 101–127.
- Pandya, D., Vanhoesen, G. W., & Mesulam, M. M. (1981). *Experimental Brain Research*, 42(3/4), 319–330.
- Patterson, K., Lambon Ralph, M. A., Hodges, J. R., & McClelland, J. L. (2001). Deficits in irregular past-tense verb morphology associated with degraded semantic knowledge. *Neuropsychologia*, 39, 709–724.
- Pinker, S. (1991). Rules of language. *Science*, 253, 530–535.
- Pinker, S. (1999). *Words and rules: The ingredients of language*. Harper-Collins.
- Pinker, S., & Ullman, M. (2002). The past and future of the past tense. *Trends in Cognitive Sciences*, 6(11), 456–463.
- Post, B., Marslen-Wilson, W. D., Randall, B., & Tyler, L. K. (2004). Morphological and phonological factors in the processing of English inflections. In *Paper presented at the meeting of the experimental psychology society*.
- Rauschecker, J. P., & Tian, B. (2000). Mechanisms and streams for processing of 'what' and 'where' in auditory cortex. *Proceedings of the National Academy of Science of the United States of America*, 97, 11800–11806.
- Scott, S., Blank, C., Rosen, S., & Wise, R. (2000). Identification of a pathway for intelligible speech in the left temporal lobe. *Brain*, 123, 2400–2406.
- Scott, S., & Johnsrude, I. (2003). The organisation and functional organisation of speech perception. *Trends in Neurosciences*, 26(2), 100–107.
- Stamatakis, E. A., Marslen-Wilson, W., Tyler, L. K., & Fletcher, P. (2004). Functional connectivity in fronto-temporal systems for speech and language. In *Proceedings of the cognitive neuroscience society 11th annual meeting*.
- Tyler, L. K. (1992). *Spoken language comprehension: An experimental approach to normal and disordered processing*. Cambridge, MA: MIT Press.
- Tyler, L. K., de Mornay Davies, P., Anokhina, R., Longworth, C., Randall, B., & Marslen-Wilson, W. D. (2002). Dissociations in processing past tense morphology: Neuropathology and behavioural studies. *Journal of Cognitive Neuroscience*, 14(1), 79–95.
- Tyler, L. K., Randall, B., & Marslen-Wilson, W. D. (2002). Phonology and neuropsychology of the English past tense. *Neuropsychologia*, 40, 1154–1166.
- Ullman, M. T., Corkin, S., Coppola, M., Hickok, G., Growdon, J. H., Koroshetz, W. J., et al. (1997). A neural dissociation within language: Evidence that the mental dictionary is part of declarative memory and that grammatical rules are processed by the procedural system. *Journal of Cognitive Neuroscience*, 9, 266–276.
- Wernicke, C. (1874). *Der Aphasische Symptomenkomplex eine Psychologische studie auf anatomischer basis*. Breslau: Cohn and Weigert.
- Wise, R., Scott, S., Blank, C., Mummery, C., Murphy, K., & Warburton, E. (2001). Separate neural systems within "Wernicke's area". *Brain*, 124, 83–95.
- Worsley, K. J., Marrett, S., Neelin, P., Vandal, A. C., Friston, K. J., & Evans, A. C. (1996). A unified statistical approach for determining significant signals in images of cerebral activation. *Human Brain Mapping*, 4, 58–73.
- Zatorre, R., Evans, A., Meyer, E., & Gjedde, A. (1992). Lateralisation of phonetic and pitch discrimination in speech processing. *Science*, 256, 846–849.
- Zurif, E. B. (1995). In L. Gleitman & M. Liberman (Eds.), *Invitation to cognitive science*. MIT Press.