

# Lexical retrieval constrained by sound structure: The role of the left inferior frontal gyrus

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## Abstract

Positron emission tomography was used to investigate two competing hypotheses about the role of the left inferior frontal gyrus (IFG) in word generation. One proposes a domain-specific organization, with neural activation dependent on the type of information being processed, i.e., surface sound structure or semantic. The other proposes a process-specific organization, with activation dependent on processing demands, such as the amount of selection needed to decide between competing lexical alternatives. In a novel word retrieval task, word reconstruction (WR), subjects generated real words from heard non-words by the substitution of either a vowel or consonant. Both types of lexical retrieval, informed by sound structure alone, produced activation within anterior and posterior left IFG regions. Within these regions there was greater activity for consonant WR, which is more difficult and imposes greater processing demands. These results support a process-specific organization of the anterior left IFG.

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## 1. Introduction

The retrieval of words into working memory involves activation of, and selection among, alternative candidates from the mental lexicon (Cutler & Clifton, 1999). The left inferior frontal gyrus (IFG) and adjacent premotor cortex (PMC) are involved in this process (Milner, 1964; Petersen, Fox, Posner, Mintun, & Raichle, 1989; Warburton et al., 1996), but the functional organization of these regions remains controversial (Gold & Buckner, 2002; Poldrack et al., 1999). One hypothesis proposes a domain-specific organization, where the anterior left IFG (Brodmann's areas (BA) 45/47) is specialized for the controlled processing of semantic information, whereas the more posterior left IFG and PMC (BA 44, extending into BA 6) processes only phonolog-

ical information (Poldrack et al., 1999; Wagner, Pare-Blagoev, Clark, & Poldrack, 2001). Alternatively, a process-specific organization has been proposed, where processing demands that are associated with the maintenance and the retrieval/selection of verbal information governs neural recruitment (Barde & Thompson-Schill, 2002; Gold & Buckner, 2002).

Evidence in favor of a domain-specific organization includes the observations that the anterior left IFG is activated during the processing of semantic information e.g. (Poldrack et al., 1999) and that the level of activation in this region is modulated by the extent of semantic processing (Wagner et al., 2001). In addition, activation of the posterior left IFG (BA 44) and PMC (BA 6) has been observed during tasks which depend upon processing the sound structure of information held in working memory, such as word-stem completion (Buckner, Raichle, & Petersen, 1995; Poldrack et al., 1999). A strict domain-specific organization for the IFG predicts that

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tasks that exclusively involve the controlled processing of non-semantic information should not activate the anterior left IFG and a number of studies have reported patterns of activation in keeping with this prediction, e.g. (Buckner et al., 1995; Poldrack et al., 1999).

However, activation of the anterior left IFG has been observed during phonological processing (Devlin, Matthews, & Rushworth, 2003) and similar levels of activation have been seen within this region when phonological and semantic processing have been directly compared (Barde & Thompson-Schill, 2002; Gold & Buckner, 2002). These results suggest that the anterior left IFG does not exclusively process semantic information and provide evidence in favor of a process-specific organization within the left IFG. Further evidence in favor of this type of organization comes from other studies which have shown that activation within the left IFG reflects the processing demands associated with many types of non-verbal as well as verbal stimuli, e.g. (Chein & Fiez, 2001; D'Esposito et al., 1998; Owen, 1997; Thompson-Schill, 2003).

Explicit lexical retrieval produces activation within the left IFG, e.g. (Warburton et al., 1996), and when word choice is determined by semantic criteria this activation includes the anterior left IFG (Raichle et al., 1994). Although this result has been interpreted as supporting a domain-specific organization, it may reflect processes that are common to processing both lexical and sub-lexical information. The observation of activation within the anterior left IFG during a verbal task that requires lexical retrieval—guided specifically by attention to surface sound structure and not word meaning—would provide further evidence for a process-specific organization.

To this end a laboratory task was chosen that required the subjects to retrieve a familiar word from memory where the correct response demanded attention to sound structure rather than meaning. The task, word reconstruction (WR), has been used to investigate the way in which the processing of vowels and consonants constrains lexical access in an overt lexical activation task (van Ooijen, 1996). In WR, listeners hear non-words and generate a real word by changing a single sound segment (phoneme). The non-words were constructed so that a real word could be generated by the substitution of either a vowel or a consonant; for example, *eltimate* can be changed into either *ultimate* or *estimate*. Such an experimental design was readily adapted to investigate the neural basis of cognitive processes involved in lexical retrieval based on sound structure but not meaning.

In the experiments of van Ooijen, English-speaking subjects showed asymmetric response patterns: WR proved more difficult when consonants rather than vowels had to be replaced, indexed by longer reaction times (RT), more errors and more omissions (van Ooi-

jen, 1994). Furthermore, when allowed a free choice, subjects used vowel substitution more frequently than consonant substitution. There are many vowel sounds in English, and they vary with regional accent (for example, contrast *bath* in Northern English vs Southern English pronunciations, or *not* in British vs North American English). Since vowels might simply be more variable in spoken English, further studies were carried out with other languages, where there are fewer vowels or the regional accent is not mainly expressed on the vowels. The same behavioral asymmetry was shown for speakers of Spanish, Dutch, and Japanese, languages which have widely differing phonemic repertoires (Cutler & Otake, 2002; Cutler, Sebastian-Galles, Soler-Vilageliu, & van Ooijen, 2000). The robustness of the effect across languages suggests that it is not simply a product of variability in the proportion of vowel and consonant sounds. Further, its presence in speakers of languages such as Spanish and Japanese, in which vowel sounds are acoustically very distinct (because there are fewer of them), argues against an explanation based on the acoustic closeness of vowels compared to consonants. Nor can the difference be explained in terms of the number of sounds which can potentially be changed, given that, in English, although the majority of words contain more consonants than vowels; changing consonants is still harder when the number of vowels and consonants in the non-words is equated (van Ooijen, 1996).

The advantage for vowel over consonant substitution is held to reflect two asymmetries, both of which are observed across languages. First, there is asymmetry in the number of lexical neighbours resulting from substitution of a single sound: on average, across the vocabularies in which WR experiments have been conducted, consonant substitution produces about twice as many existing lexical neighbours as vowel substitution (Cutler et al., 2000). However, the actual number of possible answers was strictly controlled in the experiments, and equated across vowels and consonants. Second, the acoustic variability within vowels and consonants is asymmetric. In general vowels have a greater intrinsic variability, that is the range of realizations for vowels in natural speech is far larger than the range of realizations for consonants, and perceptual confusion experiments show that this variability often produces misidentification (Hillenbrand, Getty, Clark, & Wheeler, 1995). As Rosner and Pickering put it, “the variability that a speaker accepts exceeds the variability of productions identified with high accuracy by a listener” (Rosner & Pickering, 1994). In consequence, listeners accrue greater experience of varying realizations for vowels and, potentially, more experience of initially mistaken categorization of vowels requiring revision of an initial hypothesis. This experience then translates into a greater readiness to alter vowels than consonants in a WR task.

Thus, WR involves controlled lexical retrieval that requires a search in the mental lexicon constrained by the sound structure of non-word cues. Non-word stimuli such as 'elimate' must be maintained in working memory and used to guide an iterative process of retrieving lexical candidates until the appropriate lexical item can be selected. This task places an emphasis on components of verbal working memory, including processes involved in the maintenance of sound-based representations as well as the retrieval and selection of relevant lexical items. Sound-based representations are held to be separate and distinct from semantic representations both in speech production (Levelt, Roelofs, & Meyer, 1999) and recognition (Gaskell & Marslen-Wilson, 2002; Norris, Cutler, McQueen, & Butterfield, submitted); support for this separation in recognition comes from priming experiments which show activation of sound-based representations in the absence of concomitant semantic-associate activation (Donselaar, van Koster, & Cutler, in press; Norris et al., submitted). Certainly no explicit semantic processing is required for the performance of WR; the task requires a decision that a particular phonological form is an existing word and not a decision about what it means. If any implicit semantic processing is involved in WR, we expected it to be matched by that involved in our control task, real-word repetition.

We predicted that, relative to real-word repetition, WR would produce activation within the left IFG and PMC. Our hypothesis was that the WR task would increase activity generally across the left IFG. Specifically, regions that on the basis of a domain-specific hypothesis have previously been considered as separate (i.e., the posterior left IFG and adjacent PMC for explicit phonological processing and the anterior left IFG for explicit semantic processing) would, we predicted, be activated in WR. This result would support a process-specific organization of the anterior left IFG in verbal tasks. We also expected the behavioral asymmetry observed between vowel and consonant WR to influence the degree to which verbal working memory processes are required to complete the task, and so we predicted that all regions within the left IFG would be sensitive to these increased processing demands, again supporting a process-specific organization for the left IFG.

## 2. Materials and methods

### 2.1. Subjects

Six right-handed volunteers (2 female), aged between 38 and 75 years, gave informed, written consent for the study. Subjects had no previous history of neurological or psychiatric disease. In particular, subjects had no history of hearing impairment and could clearly perceive

the stimuli in the scanner. All had English as their first language. The studies were approved by the Administration of Radioactive Substances Advisory Committee (Department of Health, UK) and the research ethics committees at the Hammersmith Hospital.

### 2.2. PET scanning

Scans were performed across the whole-brain volume with a CTI-Siemens (Knoxville, Tenn., USA) ECAT Exact HR++ (966) PET camera (Spinks et al., 2000). The dependent variable in functional imaging studies is the haemodynamic response: a local increase in synaptic activity is associated with increased local metabolism, coupled to an increase in regional cerebral blood flow (rCBF). Water labelled with a positron-emitting isotope of oxygen ( $\text{H}_2^{15}\text{O}$ ) was used as the tracer to demonstrate changes in rCBF, equivalent to changes in tissue concentration of  $\text{H}_2^{15}\text{O}$ . The resolution of the technique meant that the activity at the level of neural systems (i.e., local populations of many millions of synapses) was observed. Analysis involved relating changes in local tissue activity (normalized for global changes in activity between scans) to the behavioral task. Twelve estimations of rCBF were made at eight-minute intervals. The field-of-view encompassed the whole of the brain. For each scan  $\text{H}_2^{15}\text{O}$  was administered as a slow intravenous bolus, and the total counts per voxel during the build-up phase of radioactivity served as an estimate of cerebral blood flow (CBF). Data acquisition was performed in 3D mode, with the lead septa between detector rings removed, with one 90 s acquisition frame beginning at the start of the rise of the head curve. Stimuli were presented for 60 s, starting 15 s before the arrival of radiolabelled water in the brain, and covering the critical measurement period of rapid build-up of tracer in the brain over 30 s. After measured attenuation correction, images were reconstructed by filtered back projection (Hanning filter, cut-off frequency 0.5 Hz).

### 2.3. Study design

#### 2.3.1. Word reconstruction

One hundred and twenty non-words were used as stimuli for WR and these stimuli formed part of a set used previously in work by Cutler, van Ooijen, and Norris (1999). Each non-word could be changed into a real word by substituting either a vowel or consonant, e.g., *unsane* could be changed into either *insane* or *unsafe*. A further 60 real words were used for the baseline condition, which was single word repetition. Both the repeated words, and the real words formed by either vowel or consonant substitution, were matched as closely as possible across the groups for frequency and imageability using available scores from the MRC psycholinguistic database. Group scores ( $\pm$ SD) for

Thorndike–Lorge written frequency (freq) and imageability (img) are: repetition, freq = 357 ( $\pm 547$ ) and img = 522 ( $\pm 74$ ); vowel WR, freq = 348 ( $\pm 498$ ) and img = 511 ( $\pm 85$ ); and consonant WR, freq = 369 ( $\pm 925$ ) and img = 484 ( $\pm 108$ ). Non-words were divided into two lists: a ‘vowel list’ which subjects would change into real words by changing a vowel, and a ‘consonant list’ where they would perform the task by changing a consonant. The two lists were constructed to try and minimize the difference in difficulty between the two lists. This was achieved by creating the ‘vowel list’ from non-word stimuli for which, from previous work, we knew subjects would preferentially change a vowel and likewise creating the ‘consonant list’ from stimuli where subjects would usually change a consonant.

Psyscope (Macwhinney, Cohen, & Provost, 1997) was used to present stimuli aurally to subjects from a Power Mac laptop computer via Sony MDR G-62 headphones. Subjects, hearing either words or non-words, were asked to perform one of three tasks:

- (a) Repetition of real words (Rep).
- (b) Reconstruction of real words from non-words by replacement of a single vowel (vow WR).
- (c) Reconstruction of real words from non-words by replacement of a single consonant (con WR).

Twelve blocks of either real or non-words were presented for each of twelve scans per subject. No non-word or word was presented more than once. The stimuli were presented every four seconds. Reaction time (RT) was recorded by a circuit capable of measuring the time between the onsets of stimulus presentation and the subject’s articulated response, using a voice sensitive key linked to a Power Mac. Each subject’s responses were recorded using a Sony WM-D6C tape recorder and Sony ECM-MS907 microphone and analyzed subsequently for accuracy. Subjects were trained outside the scanner using a set of practice stimuli, none of which were presented during the study. They were instructed prior to each scan about which of the three tasks was to be performed next. The order of stimuli within each block was randomized and the order of tasks was randomized both within and between subjects.

#### 2.4. Data analysis

SPM99 software (Wellcome Department of Cognitive Neurology, Queen Square, London: <http://www.fil.ion.ucl.ac.uk/spm>) was used to realign the individual PET scans, forming a mean image in the process. This was then spatially transformed (normalized) into standard MNI (Montreal Neurological Institute) space (Evans et al., 1993). This transformation allowed comparisons across individuals to be made. Individual acti-

vation scans were then smoothed using an isotropic 12mm, (FWHM) Gaussian kernel to account for individual variation in gyral anatomy and to improve the signal-to-noise ratio. Specific effects were investigated using appropriate contrasts and covariates to create statistical parametric maps (SPMs) of the T-statistic, which were subsequently transformed into Z-scores. A blocked ANOVA was used with global counts as confound to remove the effect of global changes in perfusion across scans.

For the whole-brain analyses, the threshold for peak voxel activation was set at  $p < .05$  corrected for the volume of the whole-brain, except for activations that fell within the left IFG and lateral PMC, about which we had a priori hypotheses. For these activations a small volume correction was employed ([www.mrc-cbu.cam.ac.uk/Imaging/common/vol\\_corr.shtml](http://www.mrc-cbu.cam.ac.uk/Imaging/common/vol_corr.shtml)) using the volumes of Brodmann’s areas that lie within the IFG and PMC. Maps of Brodmann’s areas 6, 44, 45, and 47 were taken from an electronic atlas (Maldjian, Laurienti, Kraft, & Burdette, 2003) that contains approximations of cytoarchitectonic areas based upon the Talairach and Tournoux atlas (Talairach & Tournoux, 1988). A threshold of .05 corrected for either the combined volume of BAs 44, 45, and 47 (generated by combining individual masks) or the volume of BA 6. Clusters of activation that contained less than ten voxels were excluded.

The same atlas of Brodmann’s area maps (Maldjian et al., 2003) was also used to derive cortical region of interest masks (ROIs) to investigate further the response of the IFG and PMC during WR (Fig. 2). ROIs encompassing BAs 44, 45, and 47 in both hemispheres were used for this analysis. Brodmann’s area 6 was also investigated but, because of its large spatial extent, a lateral BA 6 mask was created. Using Analyze 7.5 (Biodynamics research unit, Mayo foundation, Rochester, USA.), the midpoint of the whole BA 6 mask along the X-axis was used to define the medial boundary of the new lateral BA 6 mask. ROIs were binarized and smoothed using an isotropic 4mm FWHM Gaussian kernel. These regions were then explored using the current data set. An ROI toolbox implemented within SPM99 was used to estimate the mean level of activation for all voxels that fell within each ROI (Brett, Anton, Valabregue, & Poline, 2002); estimates of activation were derived for (a) the main effect of WR relative to baseline, i.e., [(vow WR + con WR) – Rep] and (b) individual contrasts of vowel and consonant WR relative to baseline, i.e., [(vow WR – Rep)] and [(con WR – Rep)]. One-sample *T* tests were used to identify significant activation within these regions during WR. A repeated measures ANOVA was also performed with mean activation entered as the dependent variable and hemisphere (left and right), region and task (vowel or consonant WR) as within-subject factors.



### 3. Results

#### 3.1. Behavioral

##### 3.1.1. RTs and error rates for word reconstruction and repetition (Table 1)

There were significant differences between the behavioral performance of consonant and vowel WR. As expected, subjects made very few errors in repetition (3.3%); an analysis of variance (ANOVA) revealed significantly less errors [ $F(1,23) = 172.37$ ,  $p < .0005$ ], as well as shorter RTs [ $F(1,23) = 319.62$ ,  $p < .0005$ ] for repetition than for WR. Separate ANOVAs were carried out to compare vowel and consonant WR. This analysis showed that the numbers of errors were less [ $F(1,5) = 18.778$ ,  $p = .007$ ] and RT significantly shorter [ $F(1,5) = 7.503$ ,  $p = .041$ ] when vowels were used as compared to consonants. This result, even with an attempt to make consonant completion as easy as possible (see Section 2), is in accordance with previous results showing that substitution with vowels is performed more quickly and with fewer errors than substitution with consonants, e.g. (van Ooijen, 1994). In addition there was no correlation between the age of the subject and performance on the WR task.

##### 3.1.2. Errors types produced during WR (Table 2)

Errors during WR consisted of a failure to respond (an omission) or the production of an incorrect response. Errors involving the production of a response were sub-classified into five types: the intrusion of an inappropriate phoneme (either a vowel substitution during consonant WR or a consonant during vowel WR); the substitution of more than one phoneme; the complete removal of a phoneme; the addition of extra phonemes; and the production of a non-word. Overall, similar numbers of omissions and errors of production were observed during WR. The comparison of vowel and consonant WR demon-

strated similar numbers of omissions but greater numbers of errors of production for consonant WR ( $T = 5.13$  ( $df 5$ ),  $p = .004$ ). Comparing the distinct types of production errors in vowel and consonant WR demonstrated significantly more multiple phoneme substitutions in consonant WR ( $T = 3.71$  ( $df 5$ ),  $p = .014$ ). More non-words were also produced during consonant WR, although this difference only approached significance ( $T = 2.26$  ( $df 5$ ),  $p = .073$ ) (see Table 2).

### 4. Imaging

#### 4.1. Word reconstruction vs repetition

The contrast of WR with repetition demonstrated a predominantly left-lateralized cortical system as well as bilateral and midline cerebellar activations (Fig. 1. and Table 3). The peaks of activation within the left prefrontal cortex included the posterior IFG (pars opercularis: 25–50% confidence (Tomaiuolo et al., 1999)), the anterior IFG (BAs 45 and 47) and the left middle frontal gyrus (BA 9/46). Increased activity outside the prefrontal cortex was observed within the PMC (BA 6), the right paracingulate cortex (BA 32), the left posterior parietal cortex (BA 7), and the dorsal midbrain. Activation was also observed within the midline cerebellum and the right and left cerebellar hemispheres (VI) (Schmahmann et al., 1999).

The ROI analysis confirmed the presence of activation along the extent of the left IFG during WR (Fig. 2). Significant activation was observed in left BA 44 ( $T = 5.61$  ( $df 5$ ),  $p = .002$ ), left BA 45 ( $T = 5.50$  ( $df 5$ ),  $p = .003$ ), and left BA 47 ( $T = 2.92$  ( $df 5$ ),  $p = .033$ ), during WR. The equivalent regions in the right hemisphere showed no significant activation. In addition, left BA 6 was not activated significantly; however, right BA 6 showed significantly less activation during WR than during repetition ( $T = -4.8$  ( $df 5$ ),  $p = .005$ ).

#### 4.2. Consonants vs vowels in word reconstruction

Whole-brain analysis demonstrated that the level of neural activation within the left IFG was dependent upon whether lexical retrieval was achieved using a vowel or a consonant; the direct contrast of consonant

Table 1  
Performance data

Condition	RT (ms)	Error rate (%)
Repetition	1200	3.3
Vow WR	1983	36.7
Cons WR	2318	58.6

Table 2  
Error types during word reconstruction (% of all trials)

Condition	Omiss	Incorr Resp	Phon Intr	>1 Phon	Non-word	Rem Phon	Extra Phon	Total errors
Vow WR	21.7	15.0	4.4	6.1	4.4	.0	.0	36.7
Cons WR	26.1	32.5	6.7	14.2	10.0	.6	1.1	58.6
All WR	23.9	23.8	5.6	10.1	7.2	.3	.6	47.7

*Abbreviations:* WR, word reconstruction; Vow, vowel; Cons, consonant; Omiss, the omission of response; Incorr Resp, the production of an incorrect word/non-word; Phon Intr, Vow or Cons intrusion; >1 Phon, more than phonemic substitution; Non-word, the production of a non-word; Rem Phon, the removal of a phoneme; and Extra Phon, the insertion of an additional phoneme.

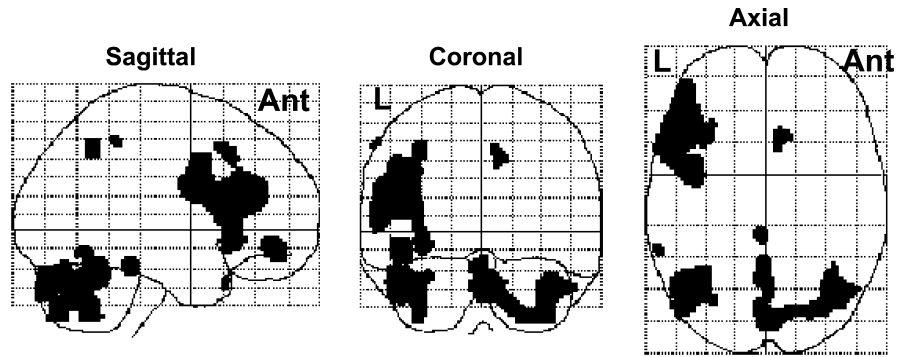


Fig. 1. Vowel and consonant WR minus repetition [(vow WR + con WR) – Rep]. Sagittal, coronal, and axial statistical parametric maps (L, left and Ant, anterior). The statistical threshold for the figure has been set at  $p < .00001$  uncorrected with a spatial extent threshold of 10 voxels.

Table 3  
Regions of significant activation for each analysis

Analysis	Region	Brodmann area/cerebellar lobule	MNI co-ordinates			T score
			x	y	z	
Main effect of WR	L MFG	9/46	-48	30	20	8.76
	L IFG	44/45	-60	20	8	7.89
	L IFG	44	-54	10	24	6.33
	L IFG	45	-54	26	16	5.68
	L IFG	47	-34	22	-6	4.9
	L IFG	47	-44	40	-8	4.41
	L PMC	6	-40	0	28	7.15
	L OFC	10	-48	48	-10	6.86
	L Paracingulate	32	10	42	44	5.21
	Mid Cerebell		0	-54	-24	7.97
	Mid Cerebell		-2	-84	-34	6.06
	R Cerebell Hem	VI	36	-62	-34	7.43
	L Cerebell Hem	VI	-48	-74	-26	6.37
	L sup PL	7	-34	56	-48	5.61
	L inf PL	7	-60	-42	50	5.27
Cons vs Vow WR	L IFG	47	-38	24	-22	4.14
	L PMC	6	-28	0	42	3.87

Approximate Brodmann's areas are taken from the Talairach and Tournoux Atlas (Talairach and Tournoux, 1988) after transforming MNI co-ordinates into Talairach space ([www.mrc-cbu.ca.ac.uk/Imaging/mnispac.html](http://www.mrc-cbu.ca.ac.uk/Imaging/mnispac.html)). Abbreviations: main effect of word reconstruction (WR) [(vow WR + con WR) – Rep], consonant (Con), vowel (Vow), left (L), right (R), middle frontal gyrus (MFG), inferior frontal gyrus (IFG), premotor cortex (PMC), orbitofrontal cortex (OFC), cerebellar hemisphere (Cerebell Hem), midline cerebellum (mid cerebell), inferior (inf), superior (sup), and parietal lobe (PL).

and vowel WR revealed greater activation for consonant WR within the anterior IFG (BA 47) (Table 3). If a more lenient threshold of .001, uncorrected for whole-brain analysis, was employed, greater activation was also observed within the left PMC. The peak of this activation fell slightly medial to the BA 6 mask employed for small volume correction.

The ROI analysis confirmed that the three anatomically defined regions within left IFG (BAs 44, 45, and 47) and left lateral BA 6 showed greater activation for consonant than vowel WR (Fig. 2). Repeated measures ANOVA revealed: a main effect of hemisphere [ $F(1,5) = 32.84, p = .002$ ], the result of greater activation in the left hemisphere; a main effect of region [ $F(1,5) = 16.14, p = .002$ ], the result of greater activation in BA 45 than in either BA 44 [ $F(1,5) = 14.6,$

$p = .012$ ] or BA 6 [ $F(1,5) = 48.5, p = .001$ ]; but, no main effect of the type of WR. An interaction between hemisphere and the type of WR was present [ $F(1,5) = 9.44, p = .039$ ], the result of greater activation for consonant WR in the left hemisphere, but no effect of the type of WR in the right hemisphere. An interaction between hemisphere and region was also present [ $F(1,5) = 10.65, p = .007$ ]. As can be seen in Fig. 2, this results from distinct effects of region in both the left [ $F(1,5) = 7.29, p = .003$ ] and the right hemispheres [ $F(1,5) = 8.45, p = .007$ ]; post hoc contrasts showed a linear effect of region in the right hemisphere [ $F(1,5) = 27.5, p = .003$ ] with activation increasing from posterior to anterior regions, but a quadratic effect of region in the left hemisphere [ $F(1,5) = 18.28, p = .008$ ] with activation peaking in BA 45. Repeating the ROI

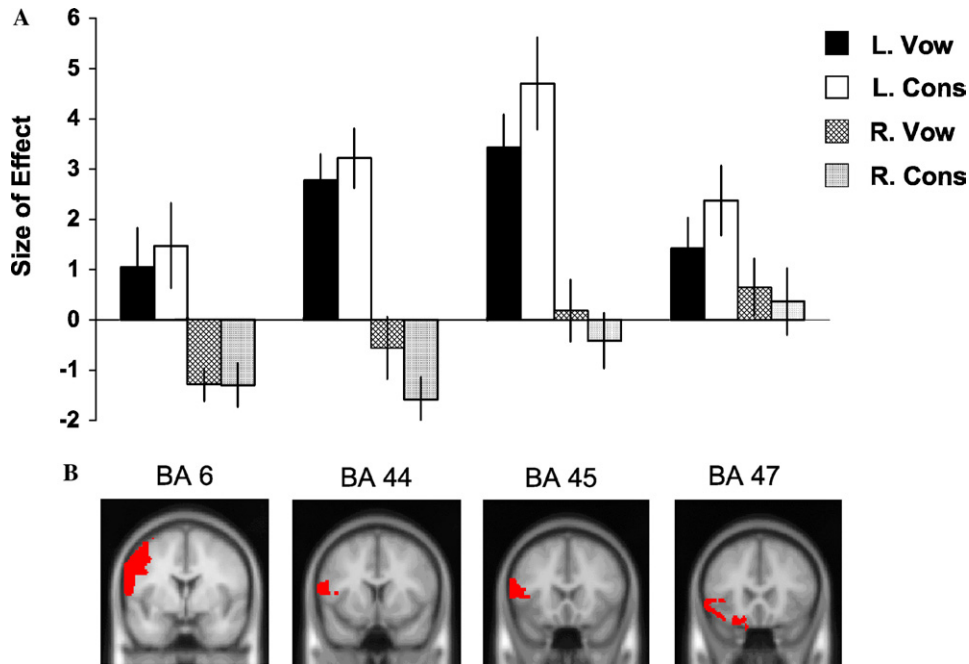


Fig. 2. (A) Plots of mean activation values ( $\pm$  the standard error of the mean) for vowel WR (Vow) and consonant WR (Con) extracted from regions of interest (ROIs) encompassing Brodmann's areas 6, 44, 45, and 47. Separate plots are given for the left (L.) and right (R.) hemispheres. (B) Representative coronal slices illustrating the anatomical locations ROIs, rendered onto an averaged group structural MRI.

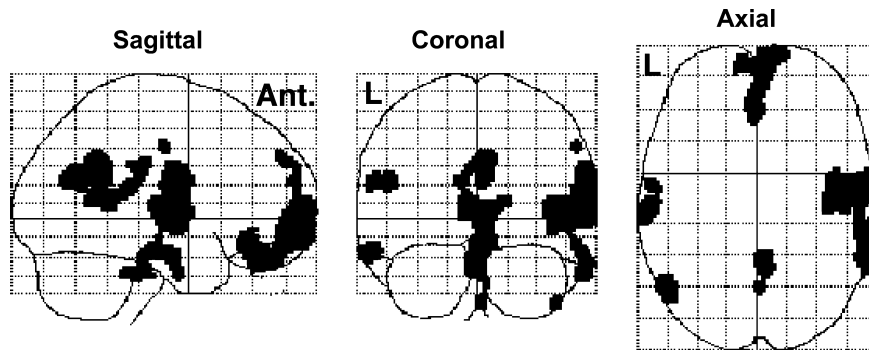


Fig. 3. Repetition minus vowel and consonant WR (Rep - [vow WR + con WR]). Sagittal, coronal and axial statistical parametric maps (L, left and Ant, anterior). The statistical threshold for the figure has been set at  $p < .00001$  uncorrected with a spatial extent threshold of 10 voxels.

analysis using the whole BA 6 as an ROI instead of limiting the ROI to lateral BA 6 produced essentially the same result. The same main effects and interactions were observed. The only difference was that the linear effect of region found in the right hemisphere did not reach significance when the entire BA 6 was used as an ROI.

#### 4.3. Repetition vs word reconstruction

When repetition was contrasted with WR, a distributed system was demonstrated (Fig. 3), with peaks of activation that included the right superior temporal gyrus (STG) (BA 22), bilateral middle temporal gyri (BA 21), bilateral frontal poles (BA 10), the left inferior parietal lobe (BA 40), and the right precuneus (BA 7).

## 5. Discussion

We have demonstrated an extensive left-lateralized, frontal cortical system involved in the explicit generation of single words during word reconstruction (WR), a controlled lexical retrieval task based on the manipulation of sub-lexical information. WR, using either vowels or consonants, produced a common system of activation that included the left IFG, with peaks in both anterior and posterior regions. Within the left IFG and adjacent PMC, activation was greater for the more difficult consonant WR task. Activation of the anterior left IFG in a task that involves no explicit semantic processing provides evidence against this region's specialization for controlled semantic processing. In addition, the in-

creased activation of left IFG during consonant relative to vowel WR suggests that the response of this region is governed by the processing demands associated with lexical retrieval, which are greater for consonant WR.

The PFC is not critical for simple automatic behavior where the relationship between stimulus and response is clear (Miller & Cohen, 2001). However, when behavior requires the guidance of internal states or intentions the contribution of the PFC becomes important (Miller & Cohen, 2001; Passingham, 1993). During this type of controlled processing information relevant to current behavior is thought to be maintained transiently, in an active form, within working memory through the firing of neurons in lateral PFC (Fuster, 1998; Goldman-Rakic, 1987). Long-term stores of information, including those for lexical and semantic knowledge, appear to be distributed in cortex posterior to the PFC (Martin & Chao, 2001; Sylvester & Shimamura, 2002). Neuroimaging work suggests that the left IFG is involved in the interaction of PFC and posterior cortex during controlled lexical retrieval, e.g. (Raichle et al., 1994; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997; Thompson-Schill, D'Esposito, & Kan, 1999; Wagner et al., 2001), as well as in the maintenance of information within working memory (D'Esposito et al., 1998; Smith & Jonides, 1998).

The way in which the left IFG interacts with posterior cortex remains controversial (Thompson-Schill, 2003; Wagner et al., 2001). During controlled verbal processing it has proved difficult to convincingly separate distinct process-specific responses within the left IFG; this results principally from problems independently controlling retrieval and selection demands (Thompson-Schill, 2003). The response of the left IFG has been shown to be sensitive to selection demands (Thompson-Schill et al., 1997; Thompson-Schill et al., 1999) and patients with lesions involving the left IFG are impaired on tasks which involve high, but not low, selection demands (Thompson-Schill et al., 1998). However, response within the left IFG has also been shown to be sensitive to retrieval demands; activity is modulated by the semantic features of retrieved information (Wagner et al., 2001) and also declines during controlled lexical retrieval, as subjects become more practiced at the task (Raichle et al., 1994).

WR requires a number of controlled processes: the maintenance of the current non-word stimulus within working memory; the retrieval of potential lexical candidates; and the rule-based selection of appropriate lexical items. As WR emphasizes phonological processing and involves no controlled semantic processing, activation of the anterior left IFG during WR provides strong evidence against a strict domain-specific organization for this region. The successful retrieval of real words in WR may involve implicit semantic processing and it could be argued that activation of the left anterior IFG reflects

such implicit processing. However, the degree of implicit semantic processing is likely to be even greater in the control task of real-word repetition and thus, this result is not compatible with a role for the anterior left IFG (BAs 45 and 47) in exclusively processing semantic information. Although WR also activated posterior IFG (BA 44) and the adjacent premotor cortex (BA 6), our results do not clarify the functional organization of these two regions as the observed activation within BA 6 and 44 during WR could be explained by either a process-specific organization or a specialization for phonological processing.

The activation of anterior left IFG during controlled phonological processing is in agreement with some studies (Barde & Thompson-Schill, 2002; Devlin et al., 2003; Gold & Buckner, 2002) but not others, e.g. (Buckner et al., 1995; Poldrack et al., 1999). The differences may result from the extent to which processing different types of information tends to recruit controlled retrieval and selection processes (Gold & Buckner, 2002). Controlled semantic processing involves focusing upon complex conceptual representations that, by their nature, often place high demands upon the retrieval and selection processes involved in mapping a stimulus to a response. In contrast, controlled phonological processing is likely to place more variable demands upon a common set of processes. Such variation can result in differential recruitment of the anterior left IFG (Gold & Buckner, 2002). For example, activation within the anterior left IFG during controlled semantic and phonological tasks was predicted by the extent to which subjects agreed on their responses, an indirect measure of the requirement for controlled retrieval and selection processes (Gold & Buckner, 2002). The type of information processed did not predict anterior left IFG activation. Activation within this region was present for both semantic and pseudoword phonological tasks, but not for real-word phonological tasks where subjects showed a high level of response consensus.

WR is a difficult task (van Ooijen, 1996) and was chosen because it places high demands upon the processes involved in lexical retrieval. As expected, subjects produced large numbers of errors; however, the failure to provide a correct answer does not necessarily imply guessing, as it might do in a choice response task. Table 2 shows that errors often involved the production of a word, albeit an inappropriate word or a non-word, providing positive evidence that subjects were engaged in the task despite their high error rates. Consonant WR is characteristically more difficult, as indexed by more errors (of all types) and longer reaction times. Activation throughout the left IFG was greater for consonant than vowel WR, which suggests that increased task difficulty produced more attempts at lexical retrieval and not a lack of effort. In addition, increased activation was observed within the anterior left IFG indicating that the processes involved in lexical retrieval generalize



across domains of information, and that processing demands, not the type of information processed, determine involvement of the left IFG in word generation.

Although WR involves both retrieval and selection demands, this task can inform the nature of the left IFG response during the selection of an appropriate lexical candidate. The number of potential lexical responses to each non-word stimulus was balanced across the vowel and consonant conditions; therefore, selection demands were balanced at the level of the final lexical selection. Thus, increased activation of the IFG observed in the consonant condition is unlikely to be related to a difference between the conditions at the final stage of lexical selection. However, vowel and consonant WR do differ in selection demands prior to this final stage, in that, across the vocabulary as a whole, consonant substitutions are more likely than vowel substitutions to produce existing lexical neighbors. Given that spoken-word recognition is known to involve automatic simultaneous activation of multiple lexical candidates, including candidates only partially supported by the input (Cutler & Clifton, 1999), this could mean that the potential competitor set activated by any WR input included more non-viable candidates in which the vowels were maintained than in which the consonants were maintained. For example, the initial portion of *unsane* could have continued with several alternative consonants (*unsavoury*, *unsaleable*, *unsayable*, *unsaintly*, etc. as well as *unsafe*), but substitution of either vowel produces fewer candidates in which the consonants are maintained (*insane*, *unscented*, etc.) These automatically activated candidates could also cause selection load by lending support to candidates for substitution (the *v* of *unsavoury*, etc.) which are in fact inappropriate. Thus differences in neural responses between vowel and consonant WR could result from varying early selection load as well as retrieval demands.

The maintenance of verbal information within working memory is also known to produce activation within the left IFG and PMC (D'Esposito et al., 1998; Smith & Jonides, 1998). Prior to the final selection of an appropriate lexical response, phonological representations of the non-word stimuli and potential lexical responses must be maintained in working memory. Therefore, activation within the left IFG and PMC could also be related to processes involved in the maintenance of information within working memory. The maintenance of verbal information can be divided into storage and rehearsal components (Baddeley, 1986, 1992). Rehearsal, a covert articulatory process, is thought to refresh the phonological store. Functional imaging studies have shown activation within the left IFG and PMC during the maintenance of verbal information (D'Esposito et al., 1998; Smith & Jonides, 1998), implicating both these regions as part of a network supporting the subvocal rehearsal of maintained information (Awh et al.,

1996; Chein & Fiez, 2001; Jonides et al., 1998; Paulesu, Frith, & Frackowiak, 1993).

The maintenance of non-words compared to that of real words produced higher levels of activation within both the anterior and posterior left IFG, suggesting an involvement of these regions in the subvocal rehearsal of non-word information (Chein & Fiez, 2001). Furthermore, in contrast to the pattern exhibited in other regions activated during the maintenance of information, activation within the posterior left IFG (dorsal BA 44) declined over the time course of the maintenance period, suggesting a differential involvement of this region early in subvocal rehearsal. Rehearsal may involve an initial phase of effortful assembly of an articulation programme, followed by its repetitive and more automatic execution (Naveh Benjamin & Jonides, 1984). Pseudo-words may place additional demands upon sublexical processing involved in this initial phase of maintenance (Levelt et al., 1999) that may account for the increased activation within the posterior left IFG during pseudo-word rehearsal. Therefore, the increased activation across the left IFG and PMC for consonant versus vowel WR could also be explained by differing demands placed upon the system involved in the subvocal rehearsal of non-word stimuli.

Comparison of vowel and consonant WR in this study also allowed an assessment of whether distinct neural subsystems exist for vowel and consonant processing within the context of the specific task demand, i.e., WR. Evidence from studies of dichotic listening, speech perception, direct cortical electrical interference, and clinical studies on patients with left hemisphere lesions suggest that the two broad classes of phonemes, vowels and consonants, have different neural representations in the speech perception system (Boatman, Hall, Goldstein, Lesser, & Gordon, 1997; Boatman, Lesser, Hall, & Gordon, 1994; Caramazza, Chialant, Capasso, & Miceli, 2000; Shankweiler & Studdert-Kennedy, 1966; van Ooijen, 1996). However, in the current study, no difference in the spatial extent of activations associated with vowel and consonant WR was observed. Of course, it is difficult to extrapolate this null result to the general issue of the neural representation of phonemes, given that subjects heard consonants and vowels in all conditions, whether words (for repetition) or non-words (for WR), so that differences in the perceptual representation of phonemes would have been masked. Nevertheless, as far as explicit manipulation of these two classes of speech sound is concerned, our results do not support a claim for neuroanatomically distinct representations.

WR involves a prolonged explicit search for a lexical candidate satisfying precise phonological requirements. Since the time of Wernicke, the mental lexicon has been commonly thought to reside within the left superior temporal cortex (Howard et al., 1992). Although in the contrast of WR against repetition no difference was

observed within the temporal lobes, a right-lateralized response in posterior STG was present in the reverse contrast of repetition against WR. As many studies have demonstrated strong symmetrical bilateral activation of superior temporal cortex when subjects listen to words and non-words (Indefrey & Cutler, in press; Mummery, Ashburner, Scott, & Wise, 1999; Petersen, Fox, Posner, Mintun, & Raichle, 1988; Wise et al., 1991), perceptual differences between WR and repetition conditions do not explain this posterior temporal lobe asymmetry. The rate of hearing stimuli was identical across tasks, and, although WR was associated with some omissions so that the rate of hearing own voice was a little higher during repetition (by 3–4 words per minute), this does not account for the right temporal lobe difference. If one assumes symmetrical bilateral superior temporal cortical activation during repetition, then the relatively higher level of activation within right temporal cortex during repetition is likely to be secondary to a relative reduction of activation in the WR conditions within superior right temporal cortex. We propose that this temporal lobe asymmetry is secondary to an attentional mechanism operating during the *explicit* lexical retrieval of WR, focusing attention upon lexical representations in the left superior temporal cortex. This hypothesis is supported by a magnetoencephalographic (MEG) study that provides evidence for differential attentional modulation of activity within the temporal cortices (Poepffel et al., 1996). When subjects ‘passively’ listened to non-words, the evoked potentials in the temporal lobes were symmetrical, but when the subjects had to explicitly determine whether each non-word contained a particular phoneme, evoked potentials on the left were significantly greater than those on the right.

In conclusion, we have demonstrated that word generation constrained by sound structure produced activation of both the anterior and posterior left IFG. Activation in both of these regions, as well as in the left PMC, was modulated by the type of phonemic substitution made to produce a real word from a non-word. These results provide evidence against a strict domain-specific organization for the left IFG. Instead they are compatible with the increasing recruitment of the anterior left IFG during lexical retrieval as process-specific demands associated with the maintenance and retrieval/selection of lexical candidates increase.

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