COGNITIVE NEUROPSYCHOLOGY, 2009, 26 (8), 685–704

Psychology Press
Taylor & Francis Group

Converging functional magnetic resonance imaging evidence for a role of the left inferior frontal lobe in semantic retention during language comprehension

A. Cris Hamilton and Randi C. Martin
Rice University, Houston, TX, USA

Philip C. Burton
University of Minnesota, Twin Cities, Minneapolis, MN, USA

Increasing evidence supports dissociable short-term memory (STM) capacities for semantic and phonological representations. Cognitive neuropsychological data suggest that damage to the left inferior and middle frontal gyri are associated with deficits of semantic STM, while damage to inferior parietal areas is associated with deficits of phonological STM. Patients identified as having semantic STM deficits are also impaired on a number of language comprehension and production paradigms. We used one such comprehension task derived from cognitive neuropsychological data to test predictions with functional magnetic resonance imaging (fMRI) using healthy participants. Using a task that required participants to make semantic anomaly judgements, we found significantly greater activation in areas of the left inferior frontal and middle frontal gyri for phrases that required maintenance of multiple words for eventual integration with a subsequent noun or verb. These data are consistent with our previous patient studies (Hanten & Martin, 2000; R. C. Martin & He, 2004; R. C. Martin & Romani, 1994) that suggest that semantic STM is associated with the left inferior and middle frontal gyri and that deficits of semantic STM have particular consequences for comprehension tasks that require maintenance of several word meanings in unintegrated form.

Keywords: Semantic short-term memory; Language comprehension; fMRI; Left inferior frontal gyrus.

A growing number of studies support a functional and anatomical dissociation between maintenance of semantic and phonological representations in short-term memory (STM; N. Martin & Saffran, 1997; R. C. Martin & He, 2004; Shivde & Thompson-Schill, 2004). The case for separable semantic and phonological capacities was originally based on findings from patients with STM deficits that were differentially impaired in the retention of phonological or semantic information. For example, R. C. Martin, Shelton, and Yaffee (1994) and R. C. Martin and He (2004) categorized patients as having either phonological or semantic STM deficits based on their performance on a

Correspondence should be addressed to A. Cris Hamilton, Rice University, 474 Sewall Hall, Houston TX 77005, USA (E-mail: a.cris.hamilton@rice.edu).

This research was supported by National Institutes of Health (NIH) Grants DC-00218 and DC-05496 to the second author at Rice University. The authors would like to thank Carissa Zimmerman for her help with the pilot work related to this study.

http://www.psypress.com/cogneuropsychology
DOI:10.1080/02643291003665688

number of STM tasks. Patients with phonological STM deficits failed to demonstrate typical phonological similarity effects on span tasks and showed typical or exaggerated lexicality effects (better recall of words than nonwords). These phonological STM patients also performed better on a category probe task (which requires maintenance of semantic information) than on a rhyme probe task (requiring phonological maintenance), suggesting a reliance on semantic information during recall. In contrast, patients with semantic STM deficits failed to show the standard lexicality effects, suggesting that they could not employ semantic information to aid recall. Moreover, these patients performed better on a rhyme probe task relative to category probe task. Thus, it was argued that patients with semantic STM deficits are unable to accurately maintain lexical–semantic representations in STM and must therefore rely on phonological representations for short-term maintenance (R. C. Martin & He, 2004). On the other hand, patients with phonological STM deficits are unable to maintain phonological representations and instead depend upon lexical–semantic representations during recall. Similar dissociations have also been reported by N. Martin and Saffran (1997), Wong and Law (2008), and Hoffman, Jefferies, Ehsan, Hopper, and Lambon Ralph (2009).

Anatomically, phonological and semantic STM deficits also appear to be related to different patterns of brain damage. Patients with semantic STM deficits have predominant damage to the left frontal lobe (Hanten & Martin, 2000; R. C. Martin & He, 2004; R. C. Martin et al., 1994) whereas patients with phonological STM deficits have more posterior lesions involving the left inferior parietal lobe (Vallar & Papagno, 1995). Thus, our working hypothesis has been that retention of semantic information relies critically on the left frontal areas, while phonological STM is localized to areas of the left parietal lobe.

Functional neuroimaging studies of semantic STM

Several studies have attempted to dissociate semantic and phonological STM capacities using functional neuroimaging. Some studies have supported dissociable anatomical regions associated with maintenance of semantic and phonological representations over a delay period (Crosson et al., 1999; Shivde & Thompson-Schill, 2004), while others have been more equivocal (Barde & Thompson-Schill, 2002; R. C. Martin, Wu, Freedman, Jackson, & Lesch, 2003).

Crosson et al. (1999) presented short lists of words and then asked participants to judge whether a series of probe words were semantically, phonologically, or orthographically related to the initial list. Several areas showed greater activation for semantic judgements, including areas in the anterior aspects of the inferior frontal gyrus (near BA 47). For the phonological judgements, more posterior areas were activated including areas around the inferior temporal-occipital junction (BA 37). Phonological judgements also activated prefrontal areas near BA 44 and 46, but these areas did not overlap with those activated in the semantic STM tasks.

Although the Crosson et al. (1999) study used a working memory task, one cannot rule out the possibility that the differential activations in the semantic, phonological, and orthographic conditions were due solely to processing stimuli along these three dimensions rather than to maintenance of representations over a short duration. A positron emission tomography (PET) study by Collette et al. (2001) more specifically addressed maintenance of both words and nonwords by manipulating load (1 vs. 3 items). Nonwords were used because they have no semantic features associated with them and consequently are thought to rely more heavily on phonological STM. In this study, the interaction between load and the word versus nonword factor (presumably tapping semantic STM rather than phonological STM) was associated with activation in the middle temporal gyrus (BA 21) and the tempoparietal junction (BA 39—angular gyrus). However, as words also have lexical–phonological representations as well as semantic representations, it is difficult to rule out the possibility that these activations might also reflect maintenance of lexical–phonological information.

R. C. Martin et al. (2003) reported a functional magnetic resonance imaging (fMRI) study examining phonological and semantic STM tasks. This study used an event-related design and specifically examined activation during a 6-second retention period and during response to a probe. Large inferior-frontal, midfrontal, and left parietal activations were implicated in STM load (i.e., in comparing maintenance of four items vs. one item) in both semantic and phonological STM tasks. The phonological STM task (in this case, a rhyme probe task) was associated with activation in left inferior parietal lobe (BA 40) and more posterior areas of the frontal lobe. The semantic STM task (which involved judging whether the probe was a synonym of a list item) also elicited frontal activation, but this activation was more anterior to the activation related to phonological STM. However, this anterior activation did not meet a strict statistical threshold when controlling for multiple comparisons, but did represent a statistical trend.

In contrast, Barde and Thompson-Schill (2002) found no differences in activation patterns between phonological and semantic STM tasks. Barde and Thompson-Schill argued that STM is organized by "process" (e.g., the type of operation being performed on given information) with no distinctions determined by "type" of material to be remembered (e.g., semantic vs. phonological information). The authors concluded that their data strongly implicate inferior frontal areas in STM, regardless of the type of information that must be maintained. However, a subsequent study by Shivde and Thompson-Schill (2004) found activation in anterior regions of the left inferior frontal gyrus (LIFG) and the left middle temporal gyrus for judgements of semantic relatedness of two words and the left superior parietal lobe for judgements of phonological relatedness. In this study, the two words on which these judgements were made were separated by a 10-s interval. Although this task does not place a particularly demanding load on STM (in terms of the number of items to be maintained), STM mechanisms would be necessary for maintenance across the 10-s delay interval. Shivde and Thompson-Schill suggested that the activation in both the anterior LIFG and the middle temporal gyrus may reflect the operation of a frontal-temporal circuit in which the function of the frontal regions is to maintain activation of semantic representations in the temporal lobe.

Other studies, while not studies of STM per se, have demonstrated dissociable regions engaged in semantic and phonological "processing" (Devlin, Matthews, & Rushworth, 2003; McDermott, Peterson, Watson, & Ojemann, 2003; Poldrack et al., 1999). For example, McDermott et al. (2003) used a task in which participants were simply "asked to attend to the relations" among 16-item lists of semantically or phonologically related words. The words either rhymed (beep, weep) or were semantically associated (bed, rest). Although this task is not explicitly a STM task, it might be assumed that the task does require some degree of support from STM. Semantically related lists were associated with activation in the left inferior frontal gyrus in BA 47 and BA 44/45, as well as activation in the left superior/middle temporal cortex in BA 22/21. Performance on the phonological lists was correlated with activation in BA 6/44, posterior to the regions activated in semantic lists, as well as activation in BA 40 and precuneus (BA 7). These data are consistent with a frontal/parietal distinction between semantic and phonological retention in STM as proposed by Martin and colleagues (R. C. Martin et al., 2003). It is also important to note that the phonological task activated posterior regions of the inferior frontal lobe associated with phonological rehearsal and speech planning. Although this latter study did not employ paradigms that are explicitly STM tasks, it would seem reasonable to assume that these tasks make at least some demand of STM. Presumably, STM is required to maintain the meanings or sounds of earlier words to relate them to later words.

Semantic STM and language comprehension

In the neuropsychological literature, Martin and colleagues (Hanten & Martin, 2000; R. C. Martin & He, 2004; R. C. Martin & Romani, 1994) have reported that deficits of phonological and semantic STM have different consequences for language processing. For example, patients with semantic STM deficits have particular difficulty detecting sentence anomalies when multiple adjectives must be maintained before subsequent integration with the noun they modify (e.g., "The *rusty*, old, red *swimsuit* was ... "; see Table 1 for additional examples). The patients had the same difficulty when multiple nouns had to be maintained until a subsequent verb was encountered to determine the noun's role with respect to the verb (e.g., "*Rocks*, trees, and shrubs *grew* in the yard"). In contrast to their performance in what was termed the *before* condition, semantic STM patients were much better at detecting semantic anomalies when an incongruous adjective appeared after a noun or anomalous nouns after the verb (*after* condition, e.g., "The *swimsuit* was old, red, and *rusty* ... " or "The gardener *grew* shrubs, trees, and *rocks* in the yard"). Multiple adjectives appearing after a noun allow for immediate integration of each adjective with the noun into a proposition. Likewise, multiple nouns appearing after a verb can be immediately assigned their role with respect to the verb as each noun is encountered. Given these data, R. C. Martin and Romani reasoned that delayed integration in the before condition placed a greater demand on semantic STM.

In addition to manipulating delayed versus immediate integration, R. C. Martin and Romani (1994) and R. C. Martin and He (2004) also manipulated the number of adjectives to be integrated. Specifically, one, two, or three adjectives (or nouns) appeared before or after the noun (or verb). Figure 1, adapted from R. C. Martin and Romani (1994), demonstrates the different patterns of performance for patients with phonological STM deficits compared with semantic STM deficits on this task. Figure 1a presents reaction time data from healthy control participants who demonstrated a significant Before/After × "Load" interaction, whereby reaction times increased as a function of the number of adjectives to be maintained, but only in the before condition (reaction times for anomaly decisions were measured from the onset of the anomalous word and from the onset of the corresponding word in the sensible sentences). Figures 1b and 1c present accuracy data for 2 patients with semantic STM deficits. Apparent in patients with semantic STM deficits is the exaggerated effect of load in the before condition. While these patients are quite accurate for one adjective (near 90% accuracy for both patients), their accuracy declines dramatically when two or three adjectives must be maintained for integration in the before condition. Importantly, this effect is not apparent in the after condition. Moreover, the exaggerated effect of load (i.e., number of propositions to be maintained) in the before condition is not apparent for patient E.A., who has a phonological STM deficit (Figure 1d).

It is also important to note that when only one adjective was required to be integrated in either the before or the after condition, reaction times among healthy control participants were equivalent in both conditions. Thus, it is difficult to attribute any differences in the before versus after condition to differences in semantic processing

Table 1. *Examples of language comprehension stimuli from R. C. Martin and Romani (1994)*

		Sensible	*Anomalous*
Before/delayed integration (greater semantic STM demands)	Adjective noun phrases	The *rusty, old, red* **wagon** ...	The *rusty, old, red* **swimsuit** ...
	Noun verb phrases	The *flowers, trees,* and *shrubs* **grew** ...	The *rocks, trees*, and *shrubs* **grew** ...
After/immediate integration (fewer semantic STM demands)	Adjective noun phrases	The **wagon** was *old, red* and *rusty* ...	The **swimsuit** was *old, red* and *rusty* ...
	Noun verb phrases	They **grew** *shrubs, trees* and *flowers* ...	They **grew** *shrubs, trees* and *rocks* ...

Note: STM = short-term memory.

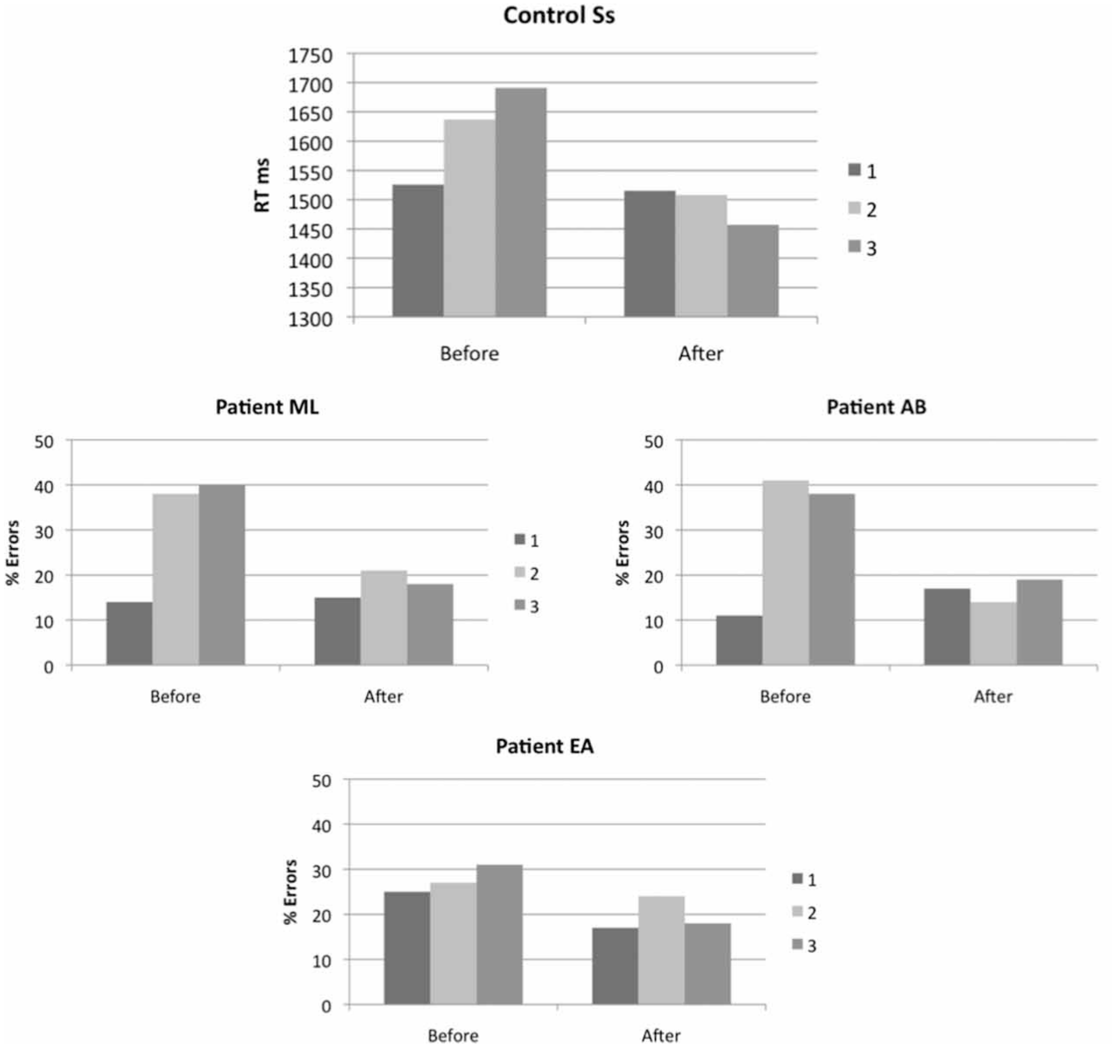

Figure 1. *Sentence anomaly task. (a) Reaction time data for control participants. (b) Accuracy data for semantic short-term memory (STM) patient A.B. (c) Accuracy data for semantic STM patient M.L. (d) accuracy data for phonological STM patient E.A. From "Verbal Working Memory and Sentence Comprehension: A Multiple-Components View", by R. C. Martin and C. Romani, 1994, Neuropsychology, 8, pp. 506–523. Copyright 1994, by the American Psychological Association, Inc. Adapted with Permission*

from the different sentence constructions in the before and after conditions.

CURRENT STUDY

Here we used the R. C. Martin and Romani (1994) paradigm (henceforth, the "before/after" paradigm) and fMRI to test the hypothesis that semantic STM processes can be localized to regions of the left middle and inferior frontal gyri. One advantage of the before/after paradigm is that it may provide a purer test of semantic retention than previous STM studies that used slow presentation rates and required verbatim recall, which probably promotes phonological rehearsal. The use of this task allows us to examine semantic maintenance in a situation akin to normal language processing, in which word meanings must be maintained for later integration. The emphasis on judgements of meaningfulness should direct attention to semantic maintenance. That emphasis, plus the fact that the words were presented in a rapid fashion approaching that of normal gaze durations in reading, should discourage the use of rehearsal.

The fMRI environment necessitated several modifications to the paradigm used by R. C. Martin and Romani (1994) and R. C. Martin and He (2004). Instead of presenting entire sentences, as was the case in the previous studies, only the four critical words from the adjective–noun or noun–verb phrase were presented in order to match the number and identity of the words in the before and after conditions. For example, instead of presenting the before sentence "She saw the *green*, *shining*, *bright sun*, which pleased her", we visually presented "green/shining/bright/sun". Instead of presenting the after sentence, "The *sun* was *bright*, *shining*, and *green*, which pleased her", we presented "sun/bright/shining/green". Participants were asked to make a sensibility judgement (by making a key press) based on whether the four words "go together". Both adjective–noun and noun–verb phrases were used in the before and after conditions. Previous behavioural studies (R. C. Martin & He, 2004; R. C. Martin & Romani, 1994) indicated that neither patients nor controls showed significant reaction time or error rate differences for the two types of phrases, and, thus, we had no a priori hypotheses concerning any differences in working memory demand between adjective–noun phrases and noun–verb phrases.

Our principal concern for this study was the contrast between the before and after conditions. Based on lesion data and previously reported functional neuroimaging results, we predicted that areas of the left middle and inferior frontal gyri previously associated with increasing STM load would show greater activation in the before condition than in the after condition. Moreover, given that this task is thought to place particular demands on semantic STM, we wanted to determine whether the before condition would elicit greater activation in areas previously reported to be associated with short-term semantic maintenance. Specifically, the before condition should engage areas of the left inferior frontal lobe reported in previous neuroimaging studies of semantic STM.

Of further interest were left inferior parietal areas, which are implicated in phonological STM. Given that phonological STM deficits do not appear sufficient to cause deficits in sentence comprehension (Butterworth, Campbell, & Howard, 1986; Hanten & Martin, 2000; Waters, Caplan, & Hildebrandt, 1991) and that patients with such deficits show interactions between before/after and load that are within normal range (Hanten & Martin, 2000; R. C. Martin & Romani, 1994), we would predict that regions associated with phonological STM would not show greater activation in the before condition than in the after condition. Also, given a model of semantic processing in which STM and control processes in the left frontal areas act upon semantic representations localized to the temporal lobe (see R. C. Martin, 2003), another prediction might be that the temporal areas will show no differences between the before and after conditions. This prediction assumes that the same amount of semantic processing occurs in both the before and after conditions, but the before condition places greater demands on maintenance processes that are supported by left frontal areas. However, if frontal regions serve to maintain the activation of semantic representations in the temporal lobe (Shivde & Thompson-Schill, 2004), then greater activation might be seen in the before than in the after condition in the temporal lobe, as several lexical–semantic representations would be maintained longer in the before condition prior to their integration into propositions. Thus, we do not have a strong prediction for the temporal region, and the analyses there should be considered exploratory.

The materials were designed such that the same words appeared in the before and after versions of each item, thus ruling out item factors as contributors to any difference in activation patterns in the two conditions. However, there was no attempt to match items across the adjective–noun and noun–verb conditions on other psycholinguistic variables such as word frequency. Similarly, there was no attempt to match the degree of anomaly between the anomalous adjective–noun and noun–verb sentences. Therefore, we cannot rule out the possibility that the any main effects of stimulus type (i.e., adjective–noun vs. noun–verb) or interactions between stimulus type and the sensible/anomalous dimension may simply result from these uncontrolled factors, rather than reflecting effects of theoretical interest. An interaction between adjective–noun/noun–verb and before/after conditions would, however, be of interest as it would suggest that differential working memory demands are involved for the two types of phrase.

Finally, it is possible that some brain regions would reflect an interaction between the before/after and sensible/anomalous conditions. In a previous event related potential (ERP) study using the before/after behavioural paradigm, we obtained such an interaction, with a larger difference in the N400 between the anomalous and sensible sentences in the after condition than in the before condition (R. C. Martin, Hamilton, Potts, & Yang, 2005). As the size of the N400 is thought to reflect the degree of semantic mismatch (Kutas & Hilyard, 1980), this finding can be related to working memory in that the anomaly should be more obvious in the after condition where the memory demands are minimized. Previous studies of sentence processing have revealed a large network of left frontal, left temporal-parietal, and right orbital-frontal regions that show greater activation for processing semantically anomalous than sensible sentences (e.g., fMRI: Ni et al., 2000; magnetoencephalography, MEG: Halgren et al., 2002). Consequently, it is possible that some areas within these broad regions would reveal an interaction between before/after and sensible/anomalous conditions, with the greatest activation in the anomalous–after condition. However, such a pattern would reflect haemodynamic response associated with semantic anomaly detection rather than reflect working memory processes and is not of principal interest here.

Method

Participants

A total of 13 participants (2 male, 11 female) were recruited from the Rice University community. Of these, 1 participant was dropped from the analysis due to excessive motion. A total of 12 participants were included in the behavioural and imaging analysis. Age ranged from 18–34 years (mean = 22.6 years). Participants were screened for history of psychiatric illness and brain trauma. All participants were right-handed. Scanning was conducted at Baylor College of Medicine's Human Neuroimaging Laboratory.

Design

A 2 (before vs. after) × 2 (adjective–noun vs. noun–verb) × 2 (sensible vs. anomalous) within-subjects design was used. For adjective–noun blocks, there were 20 trials in each of the four conditions (anomalous–before, anomalous–after, sensible–before, sensible–after). In the noun–verb blocks, there were 16 trials per condition. For the noun–verb stimuli, it was necessary to use ergative verbs that can accommodate the same nouns in the subject position for the before condition (i.e., cakes, pies, cookies, *baked*) and in the direct object position in the after condition (i.e., *baked*, cookies, pies, cakes) and maintain the thematic role of the nouns irrespective of the position in which they appear.

An event-related fMRI design with varying intertrial intervals (ITIs) of 6 s, 8 s, 10 s, and 12 s was used. Variable ITIs allow better estimation of the event-related haemodynamic response. Each participant completed a total of 4 runs, where two runs contained before stimuli and two after stimuli. Within the two before blocks and the two after blocks, one run contained adjective–noun stimuli, and the other contained noun–verb stimuli. The order of the four runs was counterbalanced across subjects.

Materials

Stimuli consisted of 40 adjective–noun stimuli and 32 noun–verb stimuli, half of which were sensible and half anomalous. All of the stimuli consisted of four words. On the anomalous trials, the anomaly appeared in the serial position farthest from the noun (e.g., *rusty*/old/red/swimsuit or swimsuit/old/red/*rusty*)—these stimuli were adapted from previous studies using this paradigm with complete sentences (cf. R. C. Martin & He, 2004; R. C. Martin & Romani, 1994). In addition, participants were presented "filler trials" in which the anomaly appeared closest to the noun (e.g., adorable/cute/*fluffy*/turtle), or between the other two adjectives (e.g., adorable/*fluffy*/cute/turtle). The position of the anomaly was manipulated to prevent participants from merely attending to the first and last words of the phrase to make their judgement. However, in the filler trials, the same words did not appear in the before and after conditions, and thus the fillers in the two conditions differed on various psycholinguistic variables. Consequently, the data from the filler trials were not included in the behavioural and imaging analyses presented here.

Procedure

Stimuli were presented using rapid serial visual presentation with each word being presented serially for 500 ms each. At the beginning of each imaging run, participants were informed which of the four conditions they would receive. Participants then indicated whether the adjectives "made sense" with the noun (or whether the nouns "made sense" with the verbs) by pressing a button box with their left hand. The order of presentation of the adjective–noun and noun–verb blocks was counterbalanced across subjects.

Data acquisition

MRI scanning was performed on a 3T, head-only, Siemens Allegra MRI scanner (software version Syngo MR 2002B, Erlangen, Germany) at the Human Neuroimaging Laboratory at Baylor College of Medicine, Houston, TX. An echo planar imaging (EPI) sequence was used with an echo time of 40 ms, a repetition time of 2,000 ms, and a 90° flip angle. Twenty-six 4-mm axial slices were collected per volume, covering the entire brain for most participants. The field of view was 220 mm, and the acquisition matrix was 64×64, resulting in a 3.44-mm in-plane resolution.

In the adjective–noun blocks, there were 304 volumes per run; in the noun–verb blocks 244 volumes were collected per run. One high-resolution structural scan consisting of 194 slices of 1 mm was acquired at the beginning of each scanning session. E-Prime was used to present stimuli and collect participants' responses. Participants viewed stimuli using a mirror mounted on the head coil that allowed a view of a projection screen located behind the scanner.

Imaging analysis

Preprocessing. Data were viewed and analysed using the AFNI software package (Cox, 1996). Preprocessing for each participant followed a script generated by the AFNI program afni_proc.py. Voxel time series were aligned to the same temporal origin using the AFNI program 3dTshift and the quintic Lagrange polynomial interpolation option. For each EPI run, each 3d volume from the input dataset was registered to the volume acquired in closest temporal proximity to the T1-weighted anatomical scan (the first volume of the first EPI scan) using the AFNI program 3dvolreg with the cubic polynomial interpolation option. A 6-mm full-width half-maximum (FWHM) Gaussian blur was then applied using AFNI's 3dmerge program. The data were then scaled in order to calculate the percentage signal change. The data were submitted to a deconvolution analysis using AFNI's 3dDeconvolve program. The deconvolution analysis estimated the impulse response function (IRF) for each unique condition according to the adjective/noun, anomalous/sensible, and before/after factors, with no assumptions regarding the shape of the function. Filler trials were modelled separately. Incorrect trials were not included in the analysis.

The deconvolution analysis produced an IRF for each condition at each voxel. The intensity values for the third and fourth time points were averaged for each condition, and these values were submitted to an analysis of variance (ANOVA) using AFNI's 3dANOVA program.

The filler trials were modelled in the deconvolution analysis, but not included in the ANOVA. The estimated haemodynamic responses were then baseline corrected such that the origin of each IRF was 0. Regions of interest (ROIs) were functionally defined based on the results of a t test contrasting task (all trials regardless of condition) with baseline (viewing a fixation cross between trials).

ROI analysis

Regions of interest were defined by first identifying the most intensely activated (peak) voxels for the task versus baseline contrast, with a very conservative threshold of $t = 7.649$ ($p = .000001$) using the AFNI program 3dmaxima. When multiple peaks exceeding this threshold were separated by less than 10 mm, the centre of mass was calculated among these peak voxels, and the ROI was calculated around this centre. This resulted in 17 peaks throughout the brain.

Using a less conservative threshold for the task versus baseline contrast ($t = 3.108$, $p = .01$), significant voxels within a 5-mm radius surrounding each peak were considered to be part of the same ROI (i.e., voxels at $p > .01$ were not included in ROI analyses). All voxels within each ROI identified above were averaged at each of seven time points for each participant. A 2 (adjectives vs. nouns) $\times$ 2 (anomalous vs. sensible) $\times$ 2 (before vs. after) $\times$ 7 (time points) repeated measures ANOVA was conducted for each ROI. Time was included as a factor in this analysis in order to statistically test whether differences among conditions in a given ROI occurred in responses that reasonably approximated the typical haemodynamic response.

Results

Behavioural data

Behavioural data were acquired from the participants while they performed the task in the scanner. However, reaction time data were not available for 1 participant due to experimenter error. A three-way ANOVA was carried out on the reaction times and error rates with before/after, sensible/anomalous, and adjective–noun/noun–verb as factors. In the reaction time analysis, the main effect of before versus after was significant, $F(1,\ 10) = 6.938$, $p = .025$; $\eta_p^2 = .410$, with longer responses in the before condition (827 ms) than in the after condition (728 ms) and with 9/11 participants showing the effect in the expected direction. Mean reaction times were identical for the adjective–noun and noun–verb stimuli (777 ms) and were nonsignificantly faster for the anomalous (763 ms) than for the sensible stimuli (793 ms), $F(1, 10) = 0.977$, $p = .346$, $\eta_p^2 = .089$. The only other effect to reach significance was a significant two-way interaction between adjective–noun/noun–verb and sensible/anomalous, $F(1,\ 10) = 5.837$, $p = .036$; $\eta_p^2 = .369$, with faster times for the anomalous (730 ms) than for the sensible stimuli (825 ms) for the adjective–noun condition but with faster times for the sensible (797 ms) than the anomalous stimuli (758 ms) for the noun–verb condition. As discussed earlier, such an interaction is difficult to interpret given that these stimuli were not matched on various dimensions across the adjective–noun and noun–verb conditions. None of the other interactions reached significance. For error rates, no effects reached significance (all ps $> .15$). The error rate in the before condition (10.5%) was similar to that in the after condition (11.2%), $t(11) = 0.25$, $p = .80$.

fMRI data—functionally defined ROIs

Table 2 presents the 17 ROIs that were identified. ROIs appear in order of magnitude of t value used to define the ROI. Coordinates are in standardized Talairach space (RAI mm). All interactions with time are for the quadratic trend, as this term would reasonably approximate the typical pattern of the haemodynamic response. Of the 17 ROIs identified, 8 of these ROIs were located in left frontal areas. ROIs yielding statistically significant interactions of time with the manipulated variables are reported below.

Three regions in the left inferior and middle frontal areas demonstrated a significant interaction of Before/After $\times$ Time. Other significant

Table 2. *ROIs identified by task versus baseline contrast*

ROI	*x*	*y*	*z*	*t* value	*Anatomical structure*	*Brodmann's area*	*Significant effects*	*F* value
1	1	23	45	10.807	R medial frontal		Time	
2	− 56	− 37	− 5	10.748	L middle temporal		Time	
3	− 39	5	33	10.339	LIFG	44		
4	− 47	38	16	10.139	LIFG/LMFG	45	Time	
5	− 42	29	2	10.08	LIFG	45	A/N × Time	F (1, 11) = 7.99, $p < .017$; $\eta_p^2 = .420$
6	45	− 33	59	9.952	R inferior parietal			
7	− 50	2	44	9.575	L middle frontal			
8	− 47	11	17	9.443	LIFG	44		
9	31	18	1	9.371	R insula			
10	− 41	27	20	8.947	LIFG/LMFG	45	A/B × Time	F (1, 11) = 11.87, $p < .005$; $\eta_p^2 = .519$
11	49	− 32	48	8.755	R inferior parietal			
12	− 23	20	3	8.187	L claustrum			
13	51	4	22	8.140	R IFG	9/44	A/S × A/B × Time	F (1, 11) = 6.11, $p = .031$; $\eta_p^2 = .435$
14	30	− 63	0	8.124	R lingual gyrus			
15	− 40	43	5	8.034	L MFG	45		
16	− 33	16	27	7.953	L MFG	44	A/B × Time	F (1, 11) = 5.75, $p = .035$; $\eta_p^2 = .343$
17	− 41	21	29	7.878	L MFG	44	A/B × Time	F (1, 11) = 8.38, $p > .015$; $\eta_p^2 = .432$

Note: Regions of interest (ROIs) appear in order of magnitude of *t* value for maxima used to identify original ROI. Coordinates are in standardized Talairach space (RAI mm). L = left. R = right. IFG = inferior frontal gyrus. MFG = middle frontal gyrus. A/N = adjective/noun. A/B = after/before. A/S = anomalous/sensible.

interactions with time were found in one ROI for the interaction of Adjective/Noun−Noun/Verb × Time and in another for the interaction of Sensible/Anomalous × Before/After × Time. Each of these ROIs is described below. *F* statistics for these significant interactions are shown in Table 2.

Left frontal ROIs

The three ROIs (ROI 10, ROI 16, and ROI 17) showing an interaction of before/after by time are depicted in Figure 2, along with their associated activation functions. (The error bars in all figures are corrected for between-subject variability as recommended by Cousineau, 2005, for within-subject designs.) For all three, significantly greater activity was observed in the before than in the after condition, consistent with our hypothesis that left frontal regions are involved in the short-term retention of semantic information. ROI 10 was located along the inferior frontal gyrus, inferior frontal sulcus, and middle frontal gyrus near BA 44 and BA 45 (coordinates, $x = -41$, $y = 27$, $z = 20$). ROI 16 was located along the left inferior frontal gyrus and sulcus (coordinates, $x = -33$, $y = 16$, $z = 27$). ROI 17 (coordinates, $x = -41$, $y = 21$, $z = 29$) was adjacent to ROI 16 along the left inferior frontal gyrus and middle frontal gyrus.

Other ROIs showing significant interactions with time

ROI 5 (coordinates, $x = -42$, $y = 29$, $z = 2$), also located along the inferior and middle frontal gyri, showed a significant interaction of Adjective/Noun × Time, with a larger response to trials in which adjective−noun phrases appeared than to those in which noun−verb phrases appeared, $F(1, 11) = 7.978$, $p = .017$, $\eta_p^2 = .420$. However,

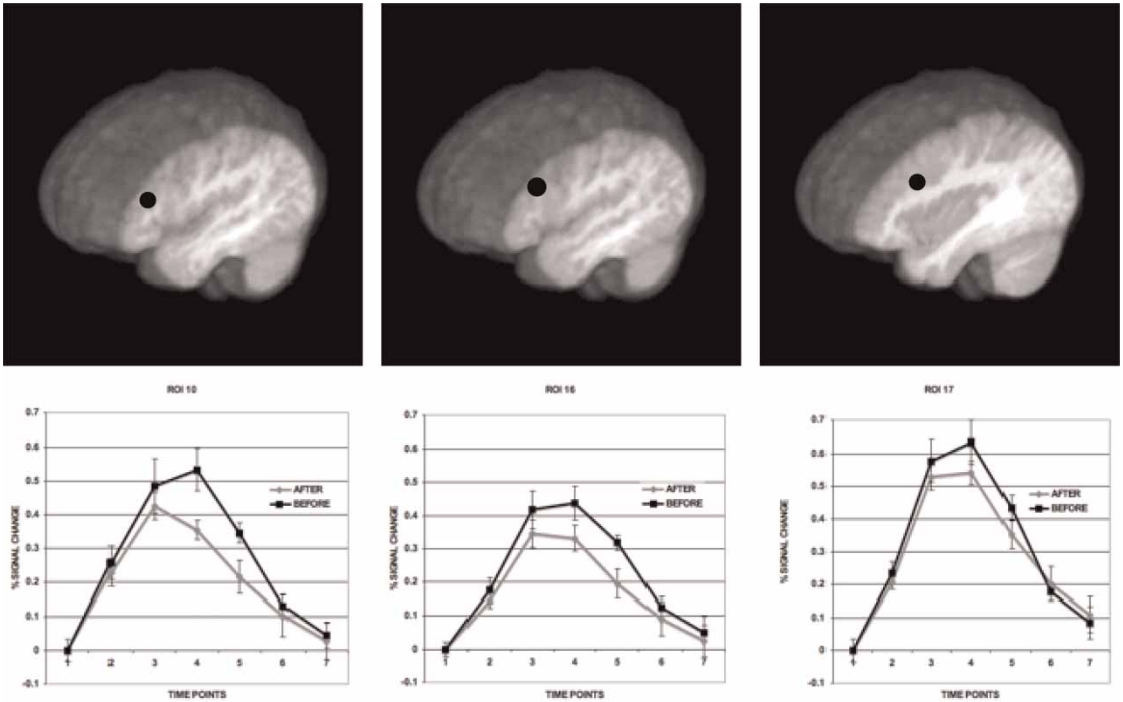

Figure 2. *Percentage signal change with time in regions of interest (ROIs) 10, 16, and 17 in left inferior frontal gyrus (LIFG) and left middle frontal gyrus (LMFG). To view a colour version of this figure, please see the online issue of the Journal.*

as discussed earlier, this difference is difficult to interpret because the items in the adjective/noun and noun/verb conditions were not matched on various psycholinguistic variables.

Finally, ROI 13 (coordinates, $x = 51$, $y = 4$, $z = 22$), located in the right inferior frontal gyrus yielded a significant Sensible/Anomalous × Before/After × Time interaction. In the before condition, activation was slightly higher in the sensible than in the anomalous condition, but this difference was not significant, $F(1,\ 11) = 1.632$, $p = .228$, $\eta_p^2 = .129$, for the Sensible/Anomalous × Time interaction. For the after condition, there was greater activation for the anomalous than for the sensible condition, which was marginally significant, $F(1,\ 11) = 4.474$, $p = .058$, $\eta_p^2 = .289$, for the Sensible/Anomalous × Time interaction. Looking at the four conditions simultaneously (as shown in Figure 3), one can see that activation was greatest in the anomalous after condition, least in the sensible after condition, and intermediate for the two before conditions. Such a pattern would correspond roughly to the degree of semantic plausibility, with the sensible after condition being the easiest to integrate and judge as plausible and the anomalous after condition being the most obviously implausible. This would be the case if we assume that the short-term memory demands make plausibility less obvious in the before condition. The association of this region with semantic plausibility is consistent with previous findings (Ni et al., 2000).

Temporal ROIs

While the LIFG is thought to be critically important for the maintenance and retrieval of semantic representations, the temporal lobes are thought to support long-term semantic representations (Hodges, Patterson, Oxbury, & Funnell, 1992; Mummery et al., 2000; Pobric, Jefferies, &

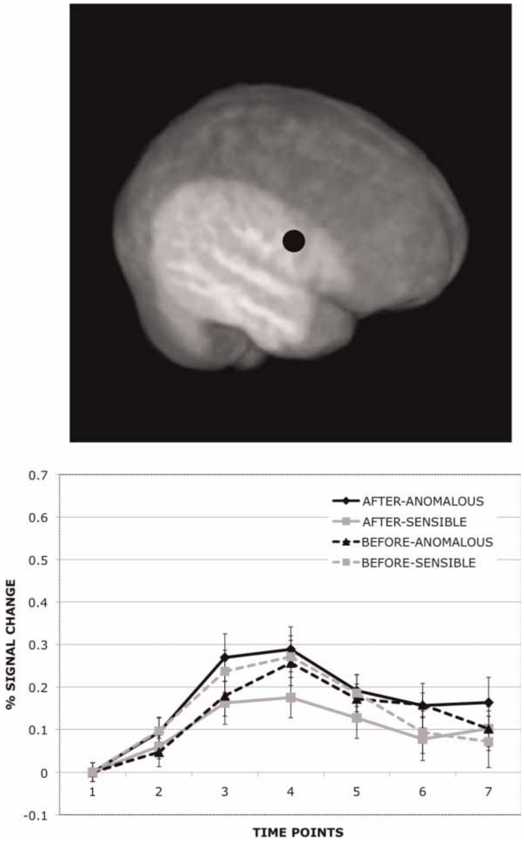

Figure 3. *Percentage signal change with time in ROI 13: right inferior frontal gyrus. To view a colour version of this figure, please see the online issue of the Journal.*

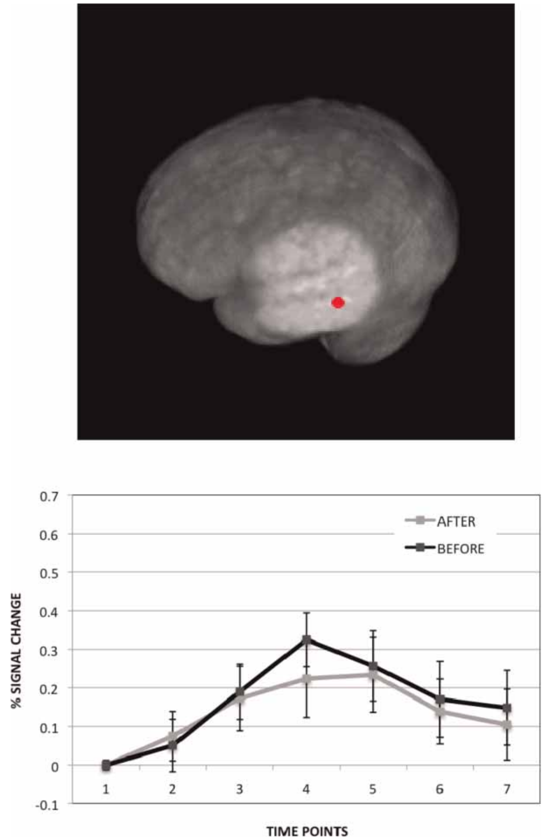

Figure 4. *Percentage signal change with time in ROI 2: left middle temporal gyrus. To view a colour version of this figure, please see the online issue of the Journal.*

Lambon Ralph, 2007). As discussed earlier, we did not have a clear prediction for this region as some have hypothesized that left frontal and temporal regions form a circuit whereby frontal regions serve to maintain the activation of semantic representations in the temporal lobe (Shivde & Thompson-Schill, 2004). Our contrast of task versus baseline revealed one area in the left middle temporal lobe near BA 21 (ROI 2 in Table 2; see Figure 4) that exceeded threshold. Although there was somewhat greater activation observed in the before than in the after condition, there was no significant interaction of Before/After × Time, $F(1, 11) = 0.947$, $p = .351$, $\eta_p^2 = .087$, in this region.

Post hoc ROI analyses

Consistent with our a priori hypotheses, none of the regions reported in Table 2 that showed significant Before/After × Time effects corresponded to areas thought to be involved in phonological STM. However, to further explore the role of phonological components in our task, we identified areas associated with phonological STM in previously published research. Specifically, we were interested in left parietal areas associated with phonological maintenance (Jonides et al., 1998; LaBar, Gitelman, Parrish, & Mesulam, 1999; Vallar & Papagno, 1995) and areas that might be involved in phonological rehearsal (Ravizza, Delgado, Chein, Becker, & Fiez, 2004). Given our hypothesis that maintenance of unintegrated adjectives or nouns places particular demands on semantic STM but not on phonological STM, we would predict no significant differences between the before and after conditions in areas associated with phonological STM. However, these post hoc analyses must be considered with caution, given that these areas did not survive the initial thresholding of task versus baseline used to functionally define ROIs in the analysis presented above.

Parietal and frontal areas associated with rehearsal. In a review of the neuroimaging literature examining verbal working memory, Becker, MacAndrew, and Fiez (1999) identified two areas within the left parietal lobe that had been previously related to the "phonological store"—an area in superior parietal lobe (mean coordinates: $x = -33$, $y = -48$, $z = 39$) and another more inferior area of the parietal lobe (mean coordinates: $x = -52$, $y = -27$, $z = 22$). Becker et al. (1999) argued that the latter, more inferior area seemed to better meet the criteria for the phonological store. Moreover, the inferior area is more consistent with the neuropsychological studies of phonological STM deficits, which have reported that the supramarginal and angular gyri are related to phonological STM (Vallar & Papagno, 1995). More recently, Ravizza et al. (2004) have suggested that the more superior region is involved in general executive functions, and the more inferior region may be involved in phonological coding as it was sensitive to a verbal/nonverbal manipulation but insensitive to load effects. However, given the association of the more inferior region with specific deficits of phonological STM in patients with good speech perception and single word production, we examined activation in this region as well.[1]

To examine the response of these areas to our task, we created spheres with a 5-voxel radius around the points of peak activation reported in the Becker et al. (1999) study. For the superior parietal area, there was no significant Before/After × Time interaction, although there was a significant four-way interaction of Adjective–Noun/Noun–Verb × Sensible/Anomalous × Before/After × Time, $F(1, 11) = 5.002$, $p = .047$, $\eta_p^2 = .313$. As discussed earlier, however, interactions involving the Adjective–Noun versus Noun–Verb factors are difficult to interpret due to possible differences in lexical factors such as frequency or differences in the degree of anomaly across these conditions. Consequently, this interaction is not considered further.

In the left inferior parietal area, which is hypothesized to be related to the phonological buffer, the response to the after conditions was actually greater than that in the before condition, although there was no interaction of Before/After × Time, $F(1, 11) = 0.06$, $p = .81$, $\eta_p^2 = .005$. However, there was an unexpected three-way interaction of Sensible/Anomalous × Before/After × Time, $F(1, 11) = 6.105$, $p = .031$, $\eta_p^2 = .357$ (see Figure 5). For the before condition, there was somewhat more activation for the sensible than for the anomalous condition, but the difference was far from statistically significant, $F(1, 11) = 0.438$, $p = .522$, $\eta_p^2 = .038$, for the interaction of Sensible/Anomalous × Time. For the after condition, greater activation was observed for the anomalous than for the sensible sentences, with the difference reaching significance, $F(1, 11) = 5.043$, $p = .046$, $\eta_p^2 = .314$. As discussed in the introduction, such a pattern might reflect the fact the anomaly is particularly noticeable in the after condition because short-term memory demands are minimal. Thus, the pattern may reflect the salience of the anomaly. However, the pattern cannot be easily explained as reflecting short-term memory demands, as the after condition should be less demanding. One possible means of

[1] Ravizza et al. (2004) cite a paper by Bartha and Benke (2003) as suggesting that an inferior temporal region (BA 37) may be involved in phonological storage as this was the common region of damage across a group of conduction aphasics. However, these patients had a variety of deficits including difficulty in repeating single words (often making phonemic paraphasias) and made some errors in single word comprehension. Thus, it is difficult to tell what aspect or aspects of their behaviour was related to damage in BA 37.

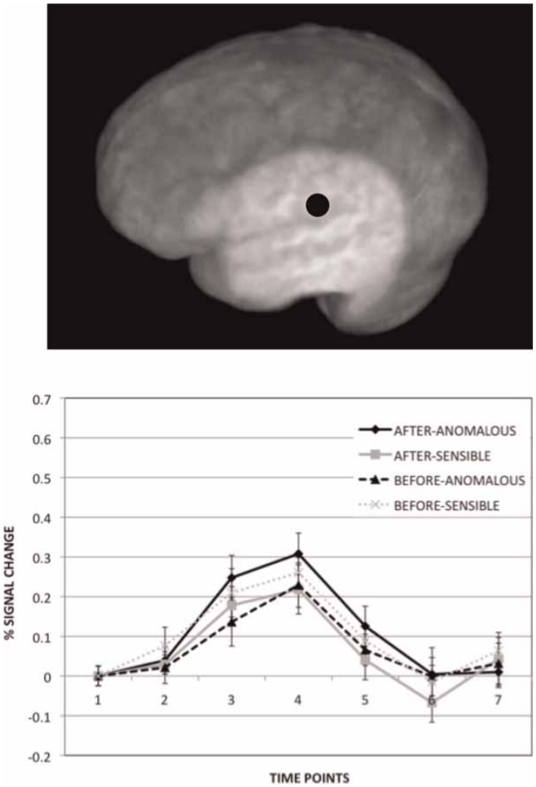

Figure 5. *Percentage signal change with time in left inferior parietal area: area identified by Becker et al. (1999) as location of phonological store. To view a colour version of this figure, please see the online issue of the Journal.*

linking the finding to phonological STM would be to assume that detection of the anomaly in the after condition led to reanalysis of the phrase, and that this reanalysis depended on a surviving phonological record. However, one might have expected such reanalysis to be even more prevalent in the anomalous before condition given that participants might have been less certain of the presence of the anomaly and more inclined to reanalyse the phrase.

In addition to the left inferior parietal lobe, the posterior aspect of BA 44 (Awh et al., 1996; Ravizza et al., 2004) has been implicated in the rehearsal and articulatory planning components of phonological short-term memory. To examine these areas, we created ROI spheres around coordinates reported to be associated with phonological rehearsal by Ravizza et al. (2004). The first was centred around coordinates $x = -46$, $y = 7$, $z = 34$ and the second around coordinates $x = -41$, $y = 17$, $z = 36$ (see Figure 6). These two frontal areas are quite close to the frontal ROIs that we have associated with semantic retention (ROIs 10, 16, and 17). Thus, it is of note that no statistically significant differences between the before and after conditions or any interactions were obtained in either of the rehearsal ROIs.

Tests of Before vs. After × *ROI*

Our initial analyses conformed to our a priori hypotheses that the before condition would place greater demands on regions in the left inferior frontal lobe previously associated with semantic short-term memory. Moreover, we predicted, and observed, no such differences in areas associated with components of phonological short-term memory (i.e., the phonological buffer or phonological rehearsal). However, to determine whether these differences between ROIs were statistically significant, we conducted follow-up ANOVAs to examine whether the difference in activation between the before and after conditions in each of the frontal ROIs differed from the activation in the areas we predicted would not show such differences. For these analyses, we computed the mean activation across the time points 3–5 for the before and after conditions in each ROI and examined the interaction of Before/After × Region. Mean activations for each of the ROIs are shown in Figure 7.

We examined these interactions for frontal ROIs 10, 16, and 17, the inferior parietal ROI, the two phonological rehearsal ROIs reported by Ravizza et al. (2004), and the temporal ROI. The results of these analyses in term of the F value for the Before/After × ROI interaction and the associated p values and effect sizes (partial eta-squared, η_p^2) appear in Table 3.

Comparisons among three left frontal ROIs. As shown in Table 3, the before/after effect did not differ significantly across the three frontal ROIs, thus indicating that these areas responded

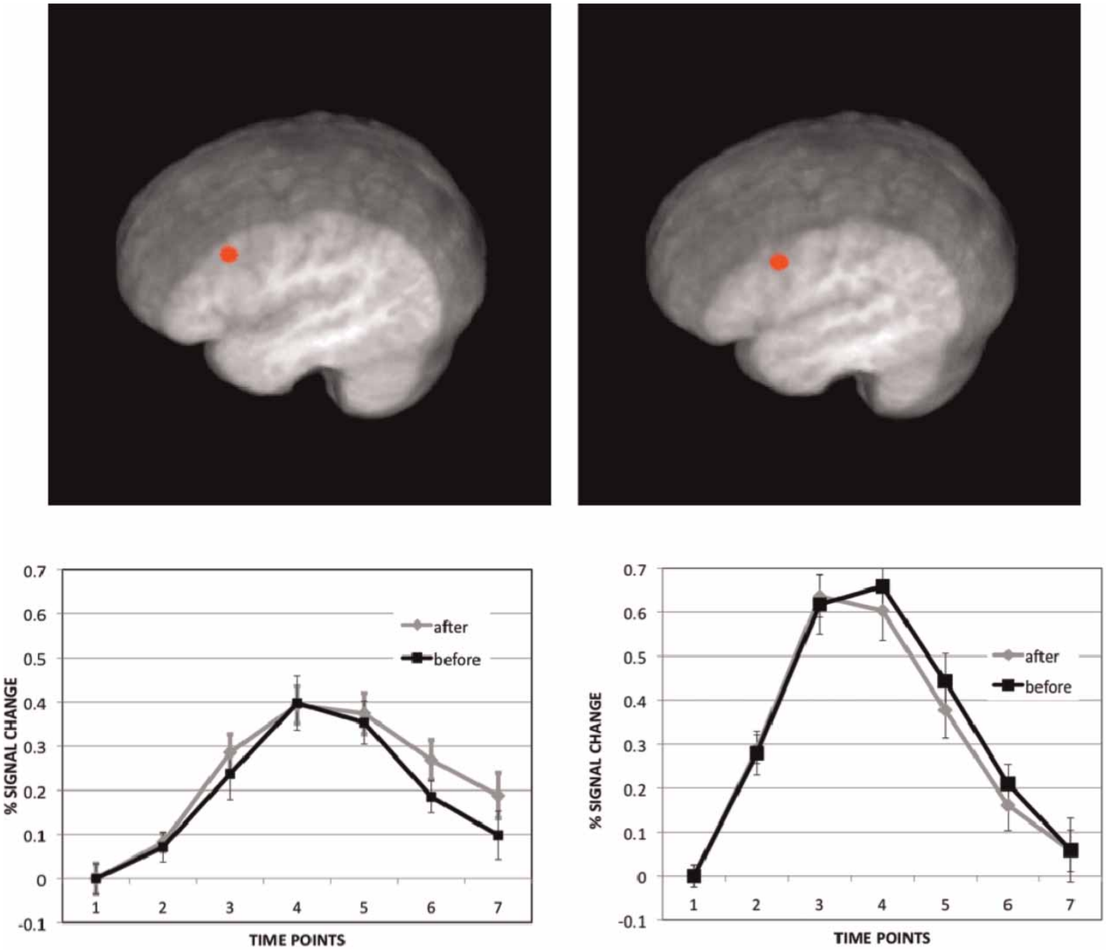

Figure 6. *Percentage signal change with time in areas identified by Ravizza et al. (2004) as being involved in phonological rehearsal. To view a colour version of this figure, please see the online issue of the Journal.*

similarly to the working memory differences in the before versus after conditions.

Interactions among left frontal ROIs and inferior parietal ROI. A statistically significant interaction was present when comparing left frontal ROI 10 with the inferior parietal ROI; however, the interaction did not reach significance in comparisons with ROIs 16 and 17. It should be noted that the before−after difference actually went in the opposite direction for this inferior parietal region, with greater activation in the after than the before condition (mean difference in signal change, after condition = .186, before condition = .165). However, when examining the difference between the after and the before conditions, there was considerable variability among subjects—range of before − after difference = −.37 to .13; main effect for before versus after, $F(1, 11) = 0.227$, $p = .643$, $\eta_p^2 = .020$—which contributed to the lack of significant interaction with the two frontal ROIs (16 and 17), which showed smaller before/after effects than ROI 10.

Comparisons among left frontal ROIs and rehearsal ROIs. The two ROIs reported by Ravizza et al.

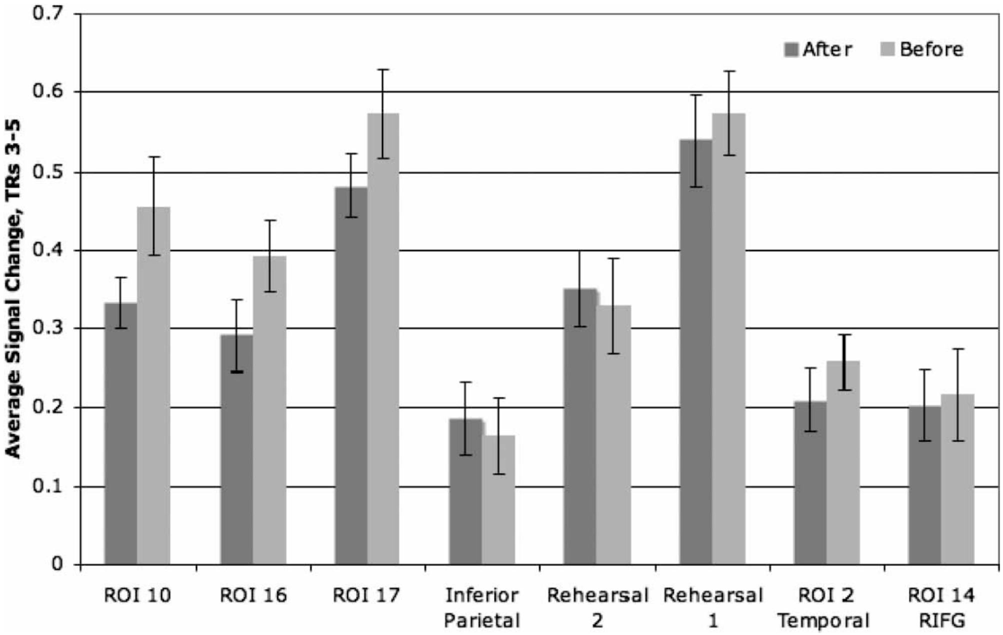

Figure 7. *Average percentage signal change, averaged over the time regions (TRs) 3–5. ROI = region of interest. RIFG = right inferior frontal gyrus.*

(2004) are termed Rehearsal 1 ($x = -46$, $y = 7$, $z = 34$) and Rehearsal 2 ($x = -41$, $y = 17$, $z = 36$). For Rehearsal 1, the interaction reached significance for ROIs 10 and 16, but failed to do so for ROI 17 (the frontal region showing the smallest before/after effect). For Rehearsal 2, the interactions reached significance for all three frontal ROIs. Thus, these data provided strong evidence that the before/after manipulation had a greater effect on these frontal regions assumed to support semantic retention than on regions argued to be involved in rehearsal.

Interactions between left frontal ROIs and temporal ROI. Unlike the case for the inferior parietal region, there was greater activation in the before

Table 3. *Before/After × ROI interactions*

	ROI 16 (frontal)	*ROI 17 (frontal)*	*Inferior parietal*	*Rehearsal 1*	*Rehearsal 2*	*Temporal ROI*
ROI 10	$F(1, 11) = 0.403$, p=.539, $\eta_p^2 = .035$	$F(1, 11) = 2.18$, $p = .168$, $\eta_p^2 = .165$	$F(1, 11) = 5.68$, $p = .036$, $\eta_p^2 = .341$	$F(1, 11) = 8.02$, $p = .016$, $\eta_p^2 = .422$	$F(1, 11) = 9.49$, $p = .010$, $\eta_p^2 = .463$	$F(1, 11) = 4.08$, $p = .069$, $\eta_p^2 = .270$
ROI 16		$F(1, 11) = 0.089$, $p = .771$, $\eta_p^2 = .008$	$F(1, 11) = 2.68$, $p = .130$, $\eta_p^2 = .196$	$F(1, 11) = 4.81$, $p = .05$, $\eta_p^2 = .304$	$F(1, 11) = 5.11$, $p = .045$, $\eta_p^2 = .317$	$F(1, 11) = 1.39$, $p = .263$, $\eta_p^2 = .112$
ROI 17			$F(1, 11) = 3.05$, $p = .108$, $\eta_p^2 = .217$	$F(1, 11) = 2.58$, $p = .136$, $\eta_p^2 = .19$	$F(1, 11) = 6.37$, $p = .028$, $\eta_p^2 = .367$	$F(1, 11) = 1.37$, $p = .267$, $\eta_p^2 = .111$

Note: ROI = region of interest.

than in the after condition in this temporal region, and the difference between these conditions in the temporal region was not substantially smaller than that for ROIs 16 and 17 (see Figure 7). For ROI 10, the interaction between Before/After × ROI was marginally significant whereas for ROIs 16 and 17, the interactions were far from significance. Thus, these data do not provide a definitive answer as to whether temporal regions show greater activation when lexical–semantic representations have to be maintained in an active state over longer periods of time.

Discussion

In this study, we used fMRI to test hypotheses generated by previous behavioural work that examined sentence comprehension deficits in patients with semantic and phonological STM deficits. R. C. Martin and Romani (1994) and R. C. Martin and He (2004) found that patients with semantic STM deficits have particular difficulty maintaining several word meanings for eventual integration but do much better when sentence structures allow for immediate integration. Using a modified version of this paradigm, we hypothesized that we should observe differences in haemodynamic response when comparing the delayed integration (i.e., the before condition) to immediate integration (i.e., the after condition). Moreover, given the patterns of brain damage previously associated with semantic STM deficits, we predicted that differences in haemodynamic response should be observed in left inferior and middle frontal areas. Consistent with our hypothesis, we observed greater activation for the before condition than for the after condition in three functionally defined ROIs along the left inferior and middle frontal gyri. All three ROIs revealed significant Before versus After × Time interactions.

All three of the these functionally defined frontal ROIs were near an area reported by R. C. Martin et al. (2003) that showed an effect of STM load using a contrast of 4-item versus 1-item memory lists (peak activation, $x = -40$, $y = 9$, $z = 27$). The observation that three of the ROIs in the present analysis are near areas involved in load effects in STM provides corroborative evidence that the maintenance of unintegrated word meanings in the before condition does, in fact, place a greater load on STM processes. In addition, the ROIs reported in the present study are very near the areas reported by R. C. Martin et al. (2003) as reflecting semantic maintenance, providing further evidence that these areas are critical in short-term maintenance of semantic representations.

These data are also consistent with the observation by R. C. Martin et al. (2003) that maintenance of semantic representations produced slightly more anterior areas of activation within the left inferior frontal gyrus than did phonological maintenance. Areas traditionally implicated in phonological rehearsal did not emerge as showing significant before versus after effects in our ROI analysis or in our post hoc analyses. Moreover, the Before/After × ROI contrasts revealed significantly greater before versus after effects in the three frontal regions than the two rehearsal regions in five out of six comparisons. Thus, it appears that the differences between the before and after conditions observed in the left inferior and middle frontal gyri do not reflect mere differences in phonological rehearsal. Of course, one cannot draw too strong a conclusion concerning the role of rehearsal in this task on the basis of null effects, and it is certainly possible that a more sensitive design might reveal activations in these areas. However, it seems clear that greater effects are seen in areas related to semantic retention.

Both cognitive neurospsychological (Vallar & Papagno, 1995) and neuroimaging data (Jonides et al., 1998) suggest that areas of the left parietal lobe, such as BA 40, are also involved in verbal working memory. Again, neither the functional ROI analysis nor our post hoc analyses found any statistically significant differences between the before and after conditions in these areas. For the inferior parietal region associated with the phonological buffer (as proposed by Becker et al., 1999), nonsignificantly greater activation was observed for the after condition than for the before condition. The only significant effect in this region was an interaction of Before/After × Anomalous/Sensible × Time, which appeared to be related to the degree of anomaly, with greatest activation for the condition in which the anomaly is most salient. It is unclear how such a pattern could be related to the demand for phonological retention.

Also of note, we found no differences in more anterior LIFG areas such as BA 47 (pars orbitalis), which have been associated with semantic processing in neuroimaging studies contrasting semantic and phonological processing (Poldrack et al., 1999). This is not surprising if one assumes that the before and after conditions do not differ in terms of overall semantic processing demands, including the amount of controlled retrieval and competition, and that it is maintenance of semantic information that differs between the two conditions.

Of further interest, the frontal areas, ROIs 10, 16, and 17, spanning areas of left inferior frontal and left middle frontal gyri, are near an area that Johnson and colleagues (Johnson et al., 2005; Raye, Johnson, Mitchell, Greene, & Johnson, 2007) have associated with "refreshing". Refreshing is conceptualized as a basic mechanism of executive control that allows one to "reactivate" representations that were previously activated by directing attention to them. Raye et al. (2007) distinguished between refreshing and rehearsal by comparing activation when thinking about a prior word versus saying it to oneself—refreshing activated areas of the middle frontal gyrus, similar to ROI 10, 16, and 17 reported here, while rehearsal activated more inferior aspects of the left frontal lobe. From this perspective, one might speculate that the delayed semantic integration in the before condition required more "refreshing" than was necessary in the after condition, which afforded immediate integration. That this task tapping semantic STM activates areas that have also been associated with executive control is interesting, given that previous work by Hamilton and Martin (2005) have suggested that executive control may be especially important in semantic short-term maintenance.

CONCLUSIONS

We report an fMRI experiment motivated by patient data that suggests that delayed integration of adjectives with nouns (and nouns with verbs) places a demand on STM and particularly on semantic STM. When participants were required to maintain three adjectives before integration with a noun (or three nouns before integration with a verb), we found greater haemodynamic response in areas along the left inferior frontal gyrus (LIFG) and left middle frontal gyrus. These data are thus consistent with previous patient data reported by R. C. Martin and Romani (1994) and R. C. Martin and He (2004).

One problem inherent in attempts to distinguish semantic and phonological STM is the difficulty in finding a task that fully dissociates the two processes. That is, phonological and semantic processing are obligatorily engaged during comprehension of words. One way that researchers have attempted to circumvent this problem is by using nonwords—letter strings that have no corresponding semantic meaning attached (e.g., Collette et al., 2001). However, the use of nonwords as a phonological task is less than ideal, as participants may attempt to associate nonwords with phonologically similar words that possess lexical and semantic representations. Also, nonwords are unfamiliar items and may require a great deal of cognitive effort for their maintenance. Based on the data reported here, the before/after paradigm might be a more appropriate task to tap semantic STM, given that it minimizes use of phonological rehearsal.

Manuscript received 26 June 2007
Revised manuscript received 21 January 2010
Revised manuscript accepted 22 January 2010
First published online 16 April 2010

REFERENCES

Awh, E., Jonides, J., Smith, E., Schumacher, E., Koeppe, R., & Katz, S. (1996). Dissociation of storage and rehearsal in verbal working memory:

Evidence from positron emission tomography. *Psychological Science*, *7*, 25–31.

Barde, L. H., & Thompson-Schill, S. L. (2002). Models of functional organization of the lateral prefrontal cortex in verbal working memory: Evidence in favor of the process model. *Journal of Cognitive Neuroscience*, *14*, 1054–1063.

Bartha, L., & Benke, T. (2003). Acute conduction aphasia: An analysis of 20 cases. *Brain and Language*, *85*, 93–108.

Becker, J. T., MacAndrew, D. K., & Fiez, J. A. (1999). A comment on the functional localization of the phonological storage subsystem of working memory. *Brain and Cognition*, *41*, 27–38.

Butterworth, B., Campbell, R., & Howard, D. (1986). The uses of short-term memory: A case study. *The Quarterly Journal of Experimental Psychology*, *38A*, 705–737.

Collette, F., Majerus, S., Van Der Linden, M., Dabe, P., Degueldre, C., Delfiore, G., et al. (2001). Contribution of lexico-semantic processes to verbal STM tasks: A PET activation study. *Memory*, *9*, 249–259.

Cousineau, D. (2005). Confidence intervals in within-subject designs: A simpler solution to Loftus and Masson's method. *Tutorial in Quantitative Methods for Psychology*, *1*, 42–45.

Cox, R. W. (1996). AFNI: Software for analysis and visualization of functional magnetic resonance neuroimages. *Computers and Biomedical Research*, *29*, 162–173.

Crosson, B., Rao, S. M., Woodley, S. J., Rosen, A. C., Bobholz, J. A., Mayer, A., et al. (1999). Mapping of semantic, phonological, and orthographic verbal working memory in normal adults with functional magnetic resonance imaging. *Neuropsychology*, *13*, 171–187.

Devlin, J. T., Matthews, P. M., & Rushworth, M. F. S. (2003). Semantic processing in the left inferior prefrontal cortex: A combined functional magnetic resonance imaging and transcranial magnetic stimulation study. *Journal of Cognitive Neuroscience*, *15*, 71–84.

Halgren, E., Dhond, R. P., Christensen, N., Van Petten, C., Marinkovic, K., Lewine, J. D., et al. (2002). N400-like magnetoencephalography response modulated by semantic context, word frequency, and lexical class in sentences. *NeuroImage*, *17*, 1101–1116.

Hamilton, A. C., & Martin, R. C. (2005). Dissociations among tasks involving inhibition: A single-case study. *Cognitive, Affective and Behavioral Neuroscience*, *5*, 1–13.

Hanten, G., & Martin, R. C. (2000). Contributions of phonological and semantic short-term memory to sentence processing: Evidence from two cases of closed-head injury in children. *Journal of Memory and Language*, *43*, 335–361.

Hodges, J. R., Patterson, K., Oxbury, S., & Funnell, E. (1992). Semantic dementia: Progressive fluent aphasia with temporal lobe atrophy. *Brain*, *115*, 1783–1806.

Hoffman, P., Jefferies, E., Ehsan, S., Hopper, S., & Lambon Ralph, M. A. (2009). Selective short-term memory deficits arise from impaired domain-general semantic control mechanisms. *Journal of Experimental Psychology: Learning, Memory and Cognition*, *35*, 137–156.

Johnson, M. K., Raye, C. L., Mitchell, K. J., Greene, E. J., Cunningham, W. A., & Sanislow (2005). Using fMRI to investigate a component process of reflection: Prefrontal correlates of refreshing a just-activated representation. *Cognitive, Affective and Behavioral Neuroscience*, *5*, 339–361.

Jonides, J., Schumacher, E. H., Smith, E. E., Koeppe, R. A., Awh, E., Reuter-Lorenz, P. A., et al. (1998). The role of parietal cortex in verbal working memory. *The Journal of Neuroscience*, *18*, 5026–5034.

Kutas, M., & Hillyard, S. A. (1980). Reading senseless sentences: Brain potentials reflect semantic incongruity. *Science*, *207*, 203–205.

LaBar, K. S., Gitelman, D. R., Parrish, T. B., & Mesulam, M.-M. (1999). Neuroanatomic overlap of working memory and spatial attention networks: A functional MRI comparison within subjects. *NeuroImage*, *10*, 695–704.

Martin, N., & Saffran, E. M. (1997). Language and auditory-verbal short-term memory impairments: Evidence for common underlying processes. *Cognitive Neuropsychology*, *14*, 641–682.

Martin, R. C. (2003). Language processing: Functional organization and neuroanatomical basis. *Annual Review of Psychology*, *54*, 55–89.

Martin, R. C., Hamilton, A. C., Potts, G. F., & Yang, C.-L. (2005, April). *Maintenance and integration of semantic representations during sentence comprehension: Electrophysiological evidence*. Poster presented at the 12th annual meeting of the Cognitive Neuroscience Society, New York.

Martin, R. C., & He, T. (2004). Semantic STM and its role in sentence processing: A replication. *Brain and Language*, *89*, 76–82.

Martin, R. C., & Romani, C. (1994). Verbal working memory and sentence comprehension: A multiple-components view. *Neuropsychology*, *8*, 506–523.

Martin, R. C., Shelton, J. R., & Yaffee, L. S. (1994). Language processing and working memory: Neuropsychological evidence for separate phonological and semantic capacities. *Journal of Memory and Language*, *33*, 83–111.

Martin, R. C., Wu, D., Freedman, M., Jackson, E. F., & Lesch, M. (2003). An event-related fMRI investigation of phonological versus semantic STM. *Journal of Neurolinguistics*, *16*, 341–360.

McDermott, K. B., Petersen, S. E., Watson, J. M., & Ojemann, J. G. (2003). A procedure for identifying regions preferentially activated by attention to semantic and phonological relations using functional magnetic resonance imaging. *Neuropsychologia*, *41*, 293–303.

Mummery, C. J., Patterson, K., Price, C. J., Ashburner, J., Frackowiak, R. S. J., & Hodges, F. R. (2000). A voxel-based morphometry study of semantic dementia: Relationship between temporal lobe atrophy and semantic memory. *Annals of Neurology*, *47*, 36–45.

Ni, W., Constable, R. T., Mencl, W. E., Pugh, K., Fulbright, R., Shaywitz, S., et al. (2000). An event-related neuroimaging study distinguishing form and content in sentence processing. *Journal of Cognitive Neuroscience*, *12*, 120–133.

Pobric, G., Jefferies, E., & Lambon Ralph, M. A. (2007). Anterior temporal lobes mediate semantic representation: Mimicking semantic dementia by using rTMS in normal participants. *Proceedings of National Academy of Science*, *104*, 20137–20141.

Poldrack, R. A., Wagner, A. D., Prull, M. W., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. E. (1999). Functional specialization for semantic and phonological processing in the left inferior cortex. *NeuroImage*, *10*, 15–35.

Ravizza, S. M., Delgado, M. D., Chein, J. M., Becker, J. T., & Fiez, J. A. (2004). Functional dissociations within the inferior parietal cortex in verbal working memory. *NeuroImage*, *22*, 562–573.

Raye, C. L., Johnson, M. K., Mitchell, K. J., Greene, E. J., & Johnson, M. R. (2007). Refreshing: A minimal executive function. *Cortex*, *43*, 135–145.

Shivde, G., & Thompson-Schill, S. L. (2004). Dissociating semantic and phonological maintenance using fMRI. *Cognitive, Affective, and Behavioral Neuroscience*, *4*, 10–19.

Vallar, G., & Papagno, C. (1995). Neuropsychological impairments of STM. In A. D. Baddeley, B. A. Wilson, & F. N. Watts (Eds.), *Handbook of memory disorders.* New York: Wiley.

Waters, G., Caplan, D., & Hildebrandt, N. (1991). On the structure and function role of auditory-verbal short-term memory in sentence comprehension: A case study. *Cognitive Neuropsychology*, *2*, 81–126.

Wong, W., & Law, S.-P. (2008). The relationship between semantic short-term memory and immediate serial recall of known and unknown words and nonwords: Data from two Chinese individuals with aphasia. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *34*, 900–917.