



Left TPJ activity in verbal working memory: Implications for storage- and sensory-specific models of short term memory

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ABSTRACT

Patients with damage to the left temporoparietal junction (TPJ) have a low verbal span without concomitant deficits in speech perception. This pattern of cognitive impairment is taken as evidence for a dedicated phonological buffer that plays little role in perception (*storage-specific account*). In contrast, other research suggests that items are maintained and perceived in the same regions (*sensory-specific account*). In an fMRI study, we demonstrate that the left TPJ does not respond in a way predicted of a phonological buffer; that is, activity in this region is not sustained during encoding or maintenance. Instead, a region in the superior temporal gyrus that has been associated with both speech perception and production demonstrated the expected profile of a store: it was more active in the verbal condition than the object condition and was active during both encoding and maintenance. These results support the sensory-specific account of short term memory rather than the storage-specific account. Based on the pattern of activity in the left TPJ, we suggest that the impairment of verbal working memory observed in patients with TPJ damage may be due to diminished attentional processes rather than reduced storage capacity.

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Introduction

A fundamental component of working memory (WM) is the maintenance of information for a brief period of time in short-term memory (STM). STM stores have been proposed to be domain-specific (Baddeley and Hitch, 1974; Cowan, 1995; Monsell, 1984); for example, separate storage systems for verbal or visuospatial information have been posited. Support for domain-specific buffers comes from studies of selective interference in which memory span is reduced by a concurrently performed task only if it uses the same code (Logie and Baddeley, 1990).

However, models of WM differ in the proposed characteristics of these domain-specific STM stores (Ruchkin et al., 2003). A central issue concerns the degree of functional overlap between perceptual and memory processes. In non-verbal domains, WM is generally considered to be *sensory specific* (Ranganath et al., 2004; Serences et al., 2009). For example, the primary visual cortex has been shown to maintain color information over a delay in a WM task (Serences et al., 2009). In contrast, the dominant account of verbal WM is *storage specific*, meaning that storage is independent from perception (Baddeley and Hitch, 1974, see Jacquemot and Scott, 2006 for a

review and an alternative viewpoint). Thus, the buffer dedicated to storing verbal information in a phonological code is not thought to be critical for speech perception (Baddeley, 1990; Logie et al., 1990). The strongest evidence for a *storage-specific* view comes from reports of patients who have impairments of verbal WM without a concomitant deficit in speech perception (Warrington and Shallice, 1969; Warrington et al., 1971; Shallice and Warrington, 1974; Basso et al., 1982; Friedrich et al., 1984; Shallice and Vallar, 1990; Belleville et al., 1992; Martin and Saffran, 1997). These patients are able to perceive speech normally, but their storage capacity for verbal information is reduced to 2–3 items (Vallar and Papagno, 1995).

Critically, damage to a non-perceptual region in the left temporoparietal junction (TPJ) of the parietal cortex, rather than primary or secondary auditory cortices in the temporal cortex, is the most commonly reported lesion site in such patients (Shallice and Vallar, 1990; Graves et al., 2005). Note that we are labeling this inferior parietal region as the TPJ rather than as the supramarginal gyrus because of its proximity to the Sylvian fissure and to distinguish it from a more dorsal region in the intraparietal sulcus that is also involved in working memory (Ravizza et al., 2004). Thus, the lesion site and the pattern of STM impairment in patients with TPJ damage are argued to support the storage-specific account of STM that claims memory and perception are independent.

While it is possible that information stored in a more abstract code such as phonology utilizes a specialized buffer for maintenance,

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neuroimaging studies have not converged with the findings of these neuropsychological studies. Neuroimaging studies of VWM would support a *storage-specific* account of STM if a region is found that is 1) *Domain-specific*: the region is more active for verbal than nonverbal stimuli, 2) *Delay-active*: the region shows sustained activation over a delay during which the information is maintained, and 3) *Post-perceptual*: the region is outside of regions involved in auditory or phonological perception such as primary/secondary auditory and motor cortex or Wernicke's area.

However, as we review below, across the many neuroimaging studies that have examined the left TPJ during VWM tasks, none has reported that pattern of activation associated with storage. Moreover, many fMRI studies have focused on load effects which we will argue do not offer a clear prediction for storage regions. In the present experiment, we will evaluate whether the pattern of brain activity in verbal and object WM tasks is supportive of the *storage-specific* or the *sensory-specific* model of STM. To characterize a region as showing a pattern of activation consistent with the role of a dedicated WM store, we will test for the following three types of effects.

Domain-specific effects

Both *storage-* and *sensory-specific* models of STM propose separate buffers for verbal and visuospatial stimuli. Numerous imaging studies have confirmed that the left TPJ is more active during verbal compared to non-verbal WM tasks (Paulesu et al., 1996; Salmon et al., 1996; Gruber and Von Cramon, 2001; Barch and Csernansky, 2007). Contrasts identifying non-verbal WM systems have used various stimuli, including faces (Barch and Csernansky, 2007), Korean letters (Paulesu et al., 1996; Salmon et al., 1996; Ravizza et al., 2004), color (Gruber and Von Cramon, 2001), or font typeface (Gruber and Von Cramon, 2001). Thus, the left TPJ fits one criterion of a verbal storage area in that it is preferentially engaged by this type of stimuli.

Delay activity

A second requirement of a region acting as a short-term store is that such a region should show sustained activity during maintenance. Many models of WM posit that items in STM will decay unless refreshed through top-down attention or articulatory rehearsal (Baddeley and Hitch, 1974; Cowan, 1995). However, imaging studies that have isolated activity during a maintenance period have generally failed to find activity in the left TPJ (Barch et al., 1996; Buchsbaum et al., 2005; Chein and Fiez, 2001; Chen and Desmond, 2005; Cohen et al., 1997; Fiebach et al., 2006; Hickok et al., 2003; Sakai et al., 2002). The lack of left TPJ activity across these studies might be due to differences in thresholds used across studies. The present study will target the left TPJ and will use both whole-brain and region-of-interest analyses in order to directly observe the pattern of activity in this area.

Post-perceptual regions

Sensory-specific accounts of STM predict that a common neural substrate will be used in perception and memory. In contrast, *storage-specific* accounts predict that regions acting as short-term stores should not typically be involved in perception. The left TPJ is not considered as part of the sensory cortex and, if this region shows domain-specificity and maintenance activity in our study, it would be good evidence for the storage-specific account.

There are several regions that fulfill the first two criteria of a verbal STM store, but these regions have been shown to be involved in speech perception and/or production. For example, a posterior region in the superior temporal gyrus (STG) has been shown to be active over a delay in WM tasks (Buchsbaum et al., 2005; Fiebach et al., 2006; Hickok et al., 2003; Sakai et al., 2002) and shown a preference for

verbal information (Paulesu et al., 1993, 1996; Salmon et al., 1996; Barch and Csernansky, 2007). However, this region in the left STG has been implicated in speech perception and production (Okada and Hickok, 2006; Acheson et al., in press) as well as WM. Thus, maintenance activity in the STG is not supportive of storage-specific accounts because this region is important for the perception of speech.

In comparison to the left TPJ, this region is located at a more posterior and inferior site than the region in the inferior parietal cortex (BA 40) that has been observed in WM studies contrasting verbal and nonverbal memory (Barch and Csernansky, 2007; Gruber and Von Cramon, 2001; Paulesu et al., 1993, 1996; Ravizza et al., 2004; Salmon et al., 1996). While the *storage-specific* account may predict activity in a perceptual region during encoding, it is unclear why a perceptual region should be engaged over the maintenance interval if the region is not involved in the computations necessary for maintaining temporary memory representations.

Load-sensitivity effects

While we do not consider a load effect to be a criterion for a short term store, an assumption in many neuroimaging studies of WM is that a region involved in maintaining items should be more active for higher loads (c.f., Cohen et al., 1997). As the number of items to be remembered increases, it seems reasonable to expect that the number of neurons required to represent them will also increase. This, in turn, may result in more blood being directed to this region to support the increased distribution of neurons supporting maintenance. Alternatively, the fMRI signal may reflect blood flow that is directed to STM regions at the rate at which the store is refreshed by articulation or attention. If so, the continuous refreshing of items in WM by articulatory rehearsal or selective attention may negate load effects in STM regions. For example, load effects in STM regions may not be apparent if only one item in the store is refreshed at any point in time. Load predictions using fMRI, then, are not straightforward for STM regions, and we do not list this as a criterion.

Load effects are not reliably observed in either the left TPJ or the left STG (Barch and Csernansky, 2007; Crottaz-Herbette et al., 2004; Reuter-Lorenz et al., 2000; Cohen et al., 1997; Jonides et al., 1997). Indeed, a meta-analysis of the verbal n-back did not find that activity in either of these regions showed reliable load effects across studies (Owen et al., 2005). Although previous studies have failed to find load effects in the left TPJ or STG, many used a block design which might mask potential load effects that were specific to one stage of the WM trial (e.g., maintenance). In the current study, we use an event-related design to determine whether load effects are present at any stage in the trial for these regions.

Summarizing the results across multiple studies, it appears that the left TPJ is preferentially engaged by verbal stimuli, but does not display load effects or delay period activity. Assessing the contribution of the left TPJ to verbal WM is critical in determining the validity of *storage-based* accounts of STM. Moreover, neuroimaging and neuropsychological studies have not provided a consistent account of left TPJ function. Resolving these conflicting results is important for understanding the particular contribution of the left TPJ in relation to the network of regions undertaking VWM.

The posterior STG fits two criteria for a verbal STM store – verbal selectivity and sustained activity over a delay – but it is also involved in speech perception (see Buchsbaum and D'Esposito, 2008 for a review). The focus of this study will be to assess load, stimulus, and delay period activity for the left TPJ and posterior STG in one experiment rather than inferring the pattern of activity across studies. Moreover, delay period activity in these two regions will be directly compared. The pattern of activity in the left TPJ and STG will help to adjudicate between the *storage-* and *sensory-specific* accounts of STM. The former predicts that the left TPJ will show domain specificity and sustained activity over a delay. In contrast, the sensory-specific

account holds that speech perception regions such as the left STG will be critical for WM.

Methods

The present study examines memory effects of load and type of information in the left TPJ and left STG using a slow, event-related design in which activity during each stage of the WM task (encoding, maintenance and retrieval) can be independently assessed. This design will provide a more sensitive test of whether the left TPJ or indeed, any non-perceptual region, fulfills all the requirements of a dedicated verbal WM buffer. To recap, these requirements include: 1) being more active for verbal than nonverbal stimuli 2) being active during the delay period and 3) peak activity residing in a region unassociated with perception. Using a serial-order recognition task, verbal memory will be compared to nonverbal memory at high and low loads (3 vs. 5 items). The verbal condition consisted of English letters whereas the non-verbal condition consisted of Korean characters. This Korean character set has the advantage of being visually similar to English letters without having an associated phonological code (Paulesu et al., 1993).

Participants

Seventeen right-handed, undergraduate students at Michigan State University (average age = 19.5 years, range = 18–24 years, 7F/10M) were paid US\$20 to participate in this experiment. All participants provided informed consent following procedures approved by the Human Research Protection Program at Michigan State University.

Stimuli

The verbal stimuli consisted 18 English letters (all the consonants except “L”) presented in 36-point Arial font. A set of Korean letters that looked least like English letters (in the estimation of the experimenters) comprised the object set. All the participants confirmed that they could not read Korean. The English and Korean letters subtended .88° and 1.3° of visual angle, respectively, and were presented in the center of the display.

Procedure

Behavioral data were collected using the E-prime software package interfaced with a fiber optic response keypad and a 1024×768 32-inch LCD monitor. Each trial lasted for 42 s (Fig. 1). At the start of each trial, participants were presented with a fixation cross for 2 s, followed by a sequence of five randomly-selected items that were displayed for 8 s (1 s/item with 600 ms between each item). No item could occur more than once in the list. In order to balance the amount of visual input in the encoding phase in the high and low load conditions, we replaced randomly chosen letters with a pound sign (#) in the low-load condition. Participants were told to ignore the pound signs and remember only the English or Korean letters.

Following presentation of the list, a rehearsal indicator (—) appeared on the screen to denote the start of 16 s maintenance interval. Participants were instructed to silently rehearse the items for the duration of the maintenance interval. After the rehearsal phase, a probe was shown (B → T), and participants had to decide whether the sequence of probe items matched the sequence in which they were presented. Probe items were in the correct sequence half of the time and, for the other half, two adjacent letters in the sequence were juxtaposed. The position in the list of the juxtaposed letters was chosen at random with equal probability. Participants responded by pressing their right index finger if the items matched and their right middle finger if they did not match. Four seconds were given to make a response, and at the end of this time the recall cue was removed. For the following 12 s participants passively viewed a fixation point.

Each participant performed 10 runs (4 min 20 s each). Each run was composed of 6 trials where stimulus type (verbal/object) and load (high/low) were randomly intermixed. Given that the design was randomized, the number of trials per condition varied from 12 to 18 with all participants completing a total of 60 trials.

fMRI data collection

Images were acquired using a GE 3 T Signa HDx scanner. High-order shimming was applied to improve the local field homogeneity. Functional data were collected using an echo planar imaging protocol, and thirty contiguous axial slices were obtained every 2 s in an interleaved manner (TR = 2 s; TE = 27.7 ms; flip angle = 77°, FOV 220 mm, voxel size = 3.44×3.44×3.4 mm³). High resolution T₁-weighted structural images with cerebrospinal fluid suppressed were acquired at the end of the session in the sagittal dimension (voxel size = 1.5×.938×1.25 mm³) to use for anatomical registration.

fMRI preprocessing and analysis

Images were corrected for motion using two iterations of a six-parameter rigid-body automated registration algorithm (AIR 5.21). The first functional image was used as the reference for motion correction. Data from participants who moved more than an average of 4 mm or rotating more than 2° in any direction were excluded. None of our participants exceeded these criteria. A baseline correction was applied by subtracting out the mean value of each voxel's time course within each run. Then, the intensities in each voxel were detrended with a simple linear regression to remove intensity changes due to scanner drift. Structural images were co-registered to the ICBM 452 reference brain using a 12-parameter affine transformation algorithm (AFNI 2.0). With the structural images as the reference, the functional images were then transformed to the standardized ICBM 452 brain with a resolution of 3.4×3.4×3.4 mm³ cubic voxels. The functional images were then smoothed with an 8 mm full width half maximum Gaussian filter.

Two separate analyses were used to examine the pattern of activity in the left TPJ – 1) a mask centered in the left TPJ based on

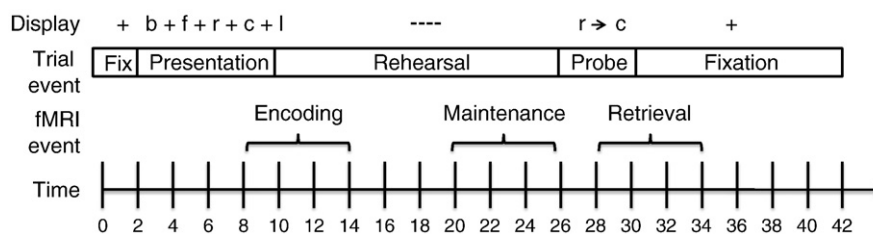


Fig. 1. Example of a verbal, high-load trial in the WM task. The top line indicates what participants saw during each stage of the trial. The trial lasts 42 s with an initial fixation cross (2 s), stimulus presentation of either 3 or 5 Korean characters or English letters (8 s), a maintenance interval (16 s), probe presentation (4 s), and a final fixation cross (12 s). In the low-load conditions, two items were randomly replaced with number signs (#). For image analysis, scans at times 8–14, 20–26, and 28–34 s were used to examine effects at encoding, maintenance, and retrieval, respectively.

findings of previous imaging studies and 2) a whole-brain analysis using contrasts of information type (Verbal high load vs. Object high load) and load (Verbal high load vs. Verbal low load). The group composite data was used in all pre-specified ROI and voxel-based statistical analysis. Analysis of the fMRI normalized signal was conducted using the Neuroimaging software package (NIS 3.6).

In the pre-specified ROI analysis, a spherical mask with a radius of 8.5 mm and a center in the inferior parietal cortex at coordinates ($x = -54, y = -27, z = 22$) was created in order to encompass peaks of activity reported across studies observing left TPJ activity in a verbal/nonverbal contrast (see Fig. 3: Barch and Csernansky, 2007; Gruber and Von Cramon, 2001; Paulesu et al., 1993; Ravizza et al., 2004; Salmon et al., 1996). A similar mask with the same size was created for the left posterior STG (see Fig. 4), but was centered at more inferior and posterior coordinates in the temporal cortex ($x = -51, y = -41, z = 15$). The mask encompassed peaks of reported activity in studies observing delay effects in the posterior STG (Buchsbau et al., 2005; Fiebach et al., 2006; Hickok et al., 2003; Sakai et al., 2002).

For these pre-specified regions of interest, we examined activity at stages of the trial using a 2 (load) \times 2 (stimulus type) repeated-measures ANOVA with an uncorrected p -value of .05. Time courses were created by averaging signal intensities across all trials in each condition. Given that activity from the previous trial was allowed time to return to baseline, percent change in signal intensity was calculated as the difference in the signal at each time point relative to the start of the trial. To assess activity at each stage, scans were selected in which the overlap of activity from previous stages was minimal and in which activity would encompass the peak of the hemodynamic response function (HRF) which typically lags by 4–6 s. For encoding, normalized signal intensity was averaged from 8 to 14 s after the onset of the trial (see Fig. 1), which corresponded to 6 s after the onset of the stimuli to 4 s after the offset of the stimuli. To observe maintenance specific activity, we averaged normalized signal intensities at the end of the rehearsal period to reduce the overlap of activity from encoding. These times corresponded to 10 s after the onset of rehearsal to the end of the rehearsal period (20–26 s after trial onset). Retrieval activity was average from normalized intensities occurring 4–12 s after the onset of the probe (28–34 s after trial onset). To ensure that the same number of scans was used to assess baseline activity as the experimental conditions, baseline activity was assessed by using the scans at the first and the last two time points.

In addition to the ANOVA analysis described above, we used a general-linear-model (GLM) approach using an assumed hemodynamic impulse response function (IRF) (see Supplemental methods). The results of the two analyses converged (see Supplemental results).

To examine a more restricted region within the left TPJ, we performed simple voxel-wise contrasts on normalized signal intensities in each voxel averaged over condition and stage (i.e., encoding, maintenance, and retrieval). Stimulus type effects were observed by comparing voxel signal intensities in the high-load verbal condition and the high-load object condition. Similarly, regions showing verbal load effects were acquired by comparing the low-load, verbal condition and high-load verbal condition. Thus, only 2 of the 4 conditions were compared in each of these simple contrasts. Given our emphasis on verbal WM, we focused on ROIs acquired in these analyses rather than regions primarily engaged in object WM. Using a Monte Carlo-based simulation program (Afn AlphaSim), we determined that a voxel-wise threshold of $p < .001$ (F -value = 16.12) and a cluster size of 13 voxels corrected the family-wise error rate to an acceptable level ($p < .05$).

Results

Behavioral data

A type (verbal/object) \times load (high/low) repeated-measures ANOVA on the accuracy data produced main effects of type ($F(1,16) = 9.27$,

$p < .05$) and load ($F(1,16) = 57.43, p < .05$). Accuracy was greatest in the verbal conditions and for low loads (Fig. 2). The interaction effect approached, but did not reach significance ($F(1,16) = 3.86, p = .067$). The same effects were obtained for RT, but the main effects were qualified by a significant interaction effect ($F(1,16) = 17.28, p < .05$). All simple comparisons were significant, however, inspection of Fig. 2 reveals that RT was especially short in the verbal, low-load condition. Thus, our design effectively manipulated WM load. Moreover, general difficulty cannot account of the activity of any region demonstrating a preference for verbal items as verbal items were recalled faster and more accurately than objects.

ROI analyses

Left TPJ-ROI analysis

Using the pre-specified ROI in the left TPJ (see Methods), we conducted a 2 \times 2 repeated measures ANOVA with information type and load as factors at each stage. The left TPJ did not show activity consistent with a phonological store (see Fig. 3) in that maintenance activity in the left TPJ did not differ from baseline (first and last two scans of a trial) in either the high-load ($t(16) = -.11, p = .917$) or low-load ($t(16) = .26, p = .797$), verbal conditions. Domain-specific effects were observed at encoding, ($F(1,16) = 24.69, p < .001$), maintenance ($F(1,16) = 10.63, p = .005$), and retrieval ($F(1,16) = 24.33, p < .001, f = 1.35$), however, the difference in activity between verbal and object conditions during maintenance was due to the continued deactivation of this region in the object conditions. Consistent with other studies, activity was not modulated by load at any stage (p -values $> .1$).

In contrast to activity during the maintenance period, activity during the retrieval period was significantly above baseline in this region in the verbal conditions (high load: $t(16) = 4.43, p = .001$; low load: $t(16) = 5.38, p < .001$). Note that these analyses are focused on the verbal conditions as a main effect of domain-specificity was observed at each stage, although activity at retrieval was above baseline in the object conditions as well. Encoding activity was not significantly above baseline levels when assessing activity across the

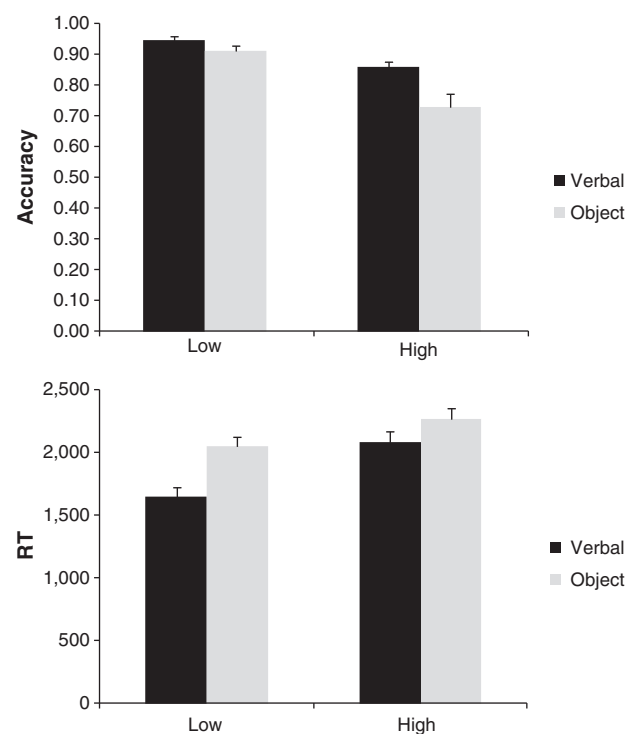


Fig. 2. Accuracy (top) and RT (bottom) from each condition.

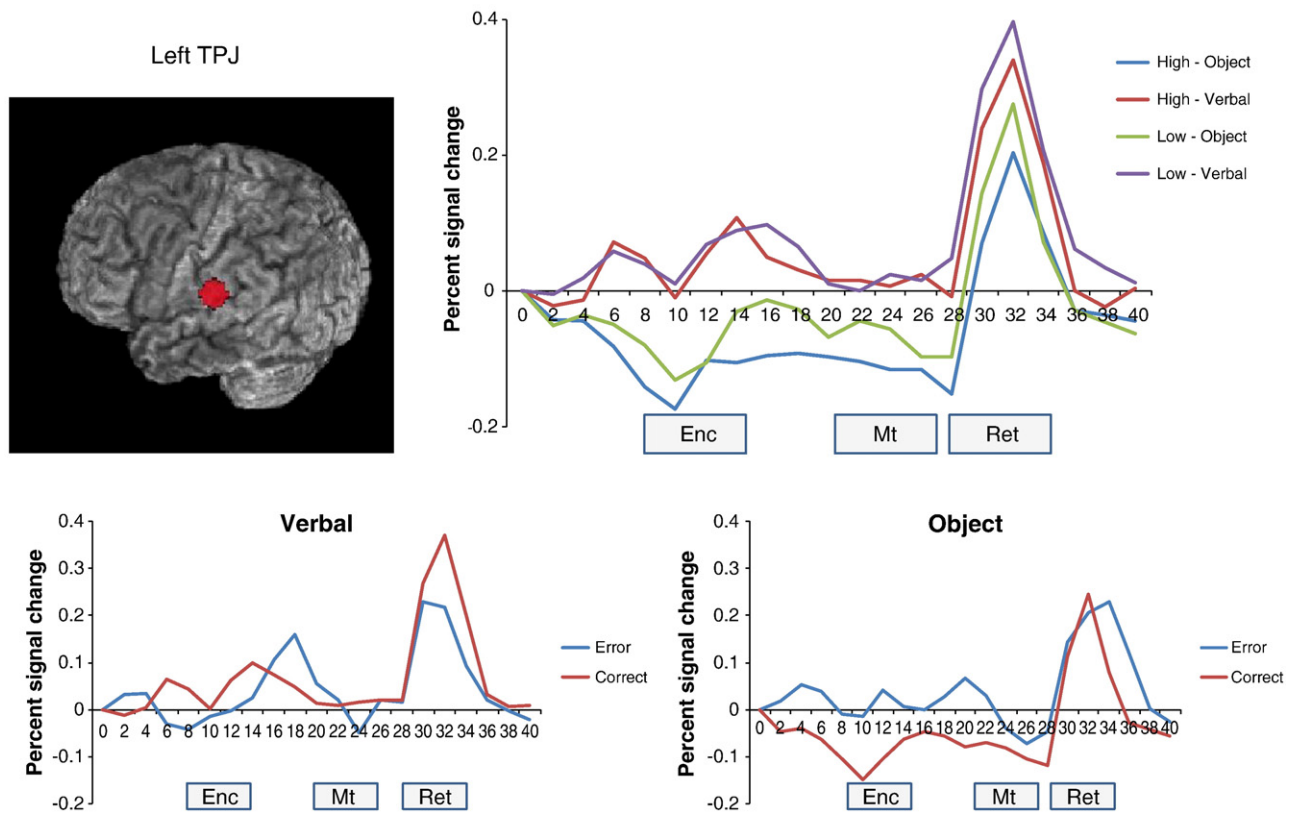


Fig. 3. Time course of activity (top right) from the pre-specified ROI in the left TPJ shown on the left side of the figure. Encoding, maintenance, and retrieval phases are shown on the x-axis. Activity during correct and error trials for the verbal conditions is shown at the lower left and the object conditions in the lower right.

whole encoding interval. Examining the time course reveals that this region exhibited two peaks of activity at the onset and offset of encoding. This dip in activity during encoding may account for the lack of significant activity compared to baseline. Activity is significantly above baseline at the end of the encoding period in the high-load verbal condition ($t(16) = 2.06$, $p = .05$), but not the low-load condition ($ps > .1$); however, this result should be interpreted cautiously as this result was not found for both conditions and would not survive the threshold used to correct for the false discovery rate.

Participants did not make enough errors to justify a statistical analysis. However, we plotted activity in the left TPJ in the verbal conditions separately for correct and error trials (Fig. 3). The overall pattern suggests that error trials were characterized by lower activity during encoding and higher activity during the early part of the maintenance period in comparison to correct trials ($n = 37$ total errors). In contrast, correct object trials were characterized by lower activity in this region than error trials.

Left posterior STG

A 2×2 repeated-measures ANOVA at each stage showed main effects of information type at encoding ($F(16) = 10.2$, $p < .01$) and retrieval ($F(16) = 5.42$, $p < .05$). Neither the main effect of load nor the interaction effect was significant at any stage ($ps > .1$). Unlike the left TPJ, activity was sustained during the maintenance interval in verbal conditions. A t -test of activity in the verbal conditions during maintenance vs. baseline was significant ($t(16) = 2.3$, $p < .05$). Note that activity appeared to also be above baseline in the object conditions; however, this effect did not reach significance ($t(16) = 1.91$, $p = .075$). Thus, the region fits both criteria of a short-term store (verbal selectivity, maintenance activity), and was not sensitive to load.

Activity in correct and error trial in the verbal conditions was plotted separately in Fig. 4. Both the left TPJ (Fig. 3) and posterior STG (Fig. 4) showed greater activity during correct trials at encoding than error trials. However, activity was sustained during correct trials during maintenance in the left STG but not in the left TPJ. Using correct trials only, we directly compared activity in the two regions at maintenance and baseline. The interaction was significant ($F(16) = 6.24$, $p < .05$), and indicated that the left STG was more active than the left TPJ during maintenance ($t(16) = 2.32$, $p < .05$) but not during baseline ($t(16) = .23$, $p = .824$). Similar to the left TPJ, greater activity of the left STG was observed in error than correct trials.

Whole brain analyses

Domain-specific effects

Our whole-brain analysis produced five regions showing domain-specific effects (Table 1; Fig. 5). One of these regions was located in the left TPJ close to the center coordinate of our pre-specified ROI. The time course of this region was virtually identical to that shown in Fig. 3; that is, it was not modulated by load and was not active during maintenance ($t(16) = -.765$, $p = .455$). Moreover, it displayed preferential activity for verbal stimuli at all 3 stages of the trial ($ps < .05$; see Table 1 and Fig. 5). A separate region centered in the temporal cortex was observed to show domain-specific effects and was located between the left TPJ and posterior STG. This region also showed a similar time course to that of the left TPJ. Unlike the posterior STG ROI that we pre-specified, this region did not show sustained activity over the delay.

Other regions showing language-specific effects included the left motor/premotor cortex. This region encompassed the face area of the left motor cortex and showed domain-specific effects at encoding that were sustained during maintenance ($t(16) = 8.28$, $p < .05$) and retrieval ($t(16) = 8.57$, $p < .05$). At encoding, this region was most responsive to verbal stimuli at high loads and the interaction effect

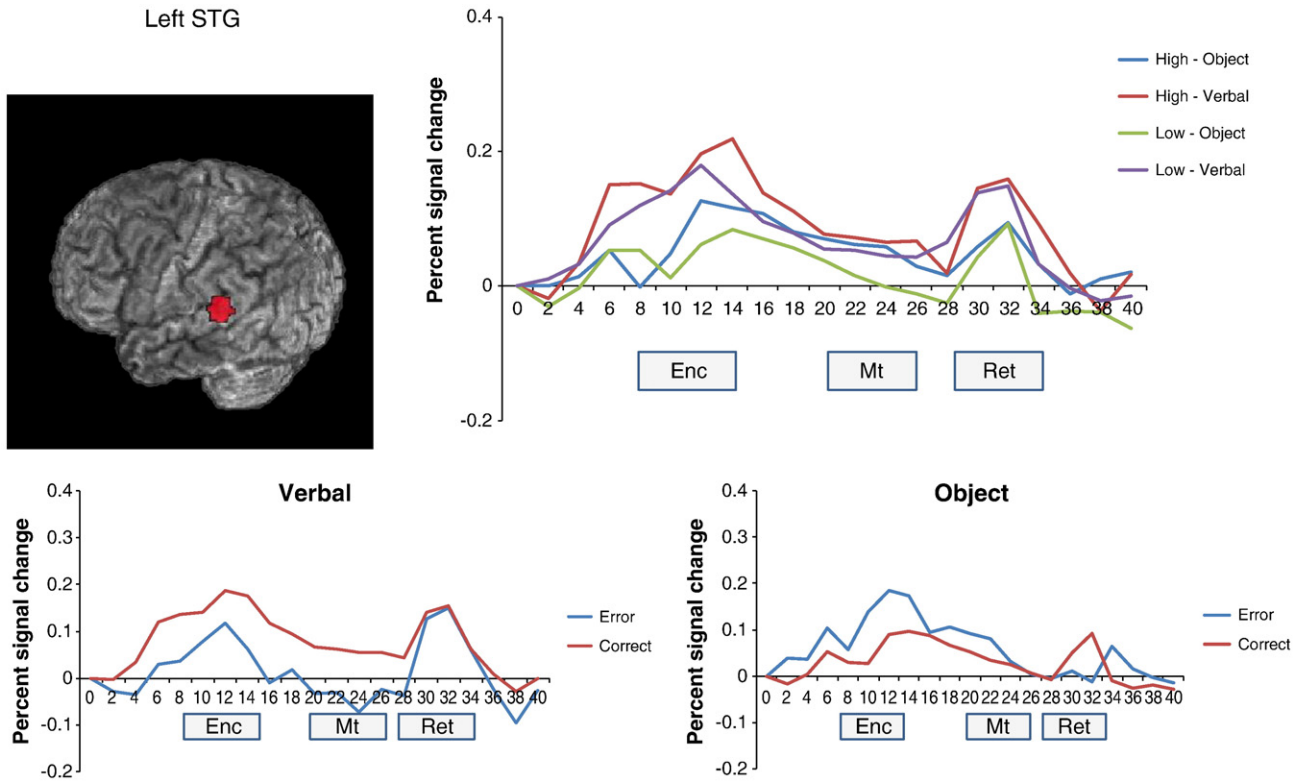


Fig. 4. Time course of activity (top right) from the pre-specified ROI in the left STG. Encoding, maintenance, and retrieval phases are shown on the x-axis. Activity during correct and error trials for the verbal conditions is shown at the lower left and the object conditions in the lower right.

was significant ($F(1,16) = 5.17, p < .05$). Significant differences in neural response were observed between the high-load verbal conditions and the high-load, object ($t(16) = 4.62, p < .05$) and low-load verbal conditions ($t(16) = 2.93, p < .05$). Activity of this region was sustained during the maintenance stage in the high-load, verbal condition ($t(16) = 3.98, p < .05$). Thus, this is consistent with this region's putative role in articulatory rehearsal.

Domain-specific effects were also observed in the left putamen, but were limited to the encoding stage. The region tended to be most active during the verbal, high-load condition compared to the other 3 conditions, but the interaction effect only approached significance ($F(1,16) = 4.36, p = .053$). Activity in this region was sustained in the high-load verbal condition and was significantly different from baseline ($t(16) = 7.01, p < .05$).

The difference in neural activity between the high-load conditions in the right amygdala was only observed during maintenance, and was driven by the deactivation of this region in the high-load, object condition (see Fig. 5). Activity in the verbal condition was not different from baseline activity during maintenance.

Load effects

Six regions displayed a load effect in the verbal conditions at encoding, maintenance, or retrieval (Table 1; Fig. 6). These were the left insula/inferior frontal gyrus, the right cerebellum, the right middle frontal gyrus, the supplementary motor area, the left motor cortex, and the left inferior/middle frontal gyrus. None of these regions was more active in the verbal condition. Instead, some regions were not sensitive to the type of stimuli while others were more active for object than

Table 1

Coordinates of peak activity during encoding, maintenance, and retrieval during simple contrasts of information type (high load conditions) or load (verbal conditions).

	Encoding			Maintenance			Retrieval			Cluster size (mm ³)	High verbal maint>baseline
	x	y	z	x	y	z	x	y	z		
<i>High verbal ≥ high object</i>											
Left putamen	-25	-6	5							3105	✓
Right amygdala				15	-4	-12				2555	✓
Left TPJ	-61	-26	22		*			*		1101	✓
Left TPJ/STG		*					-58	-35	18	747	✓
Left motor/premotor	-55	-11	22		*			*		1061	✓
<i>High verbal ≥ low verbal</i>											
Left insula/IFG	-28	-15	12							1690	✓
Right cerebellum				20	-62	-25				1887	✓
Right MFG	30	31	39	31	30	29				589, 511	✓
SMA		*		3	4	52				1297	✓
Left motor	-49	-9	52		*					1101	✓
Left IFG/MFG		*		-54	8	26	-48	14	29	5817, 747	✓

TPJ = temporoparietal junction; IFG = inferior frontal gyrus; MFG = middle frontal gyrus; SMA = supplementary motor area.

* Significant difference ($p < .05$) of this region during other stages in post-hoc tests.

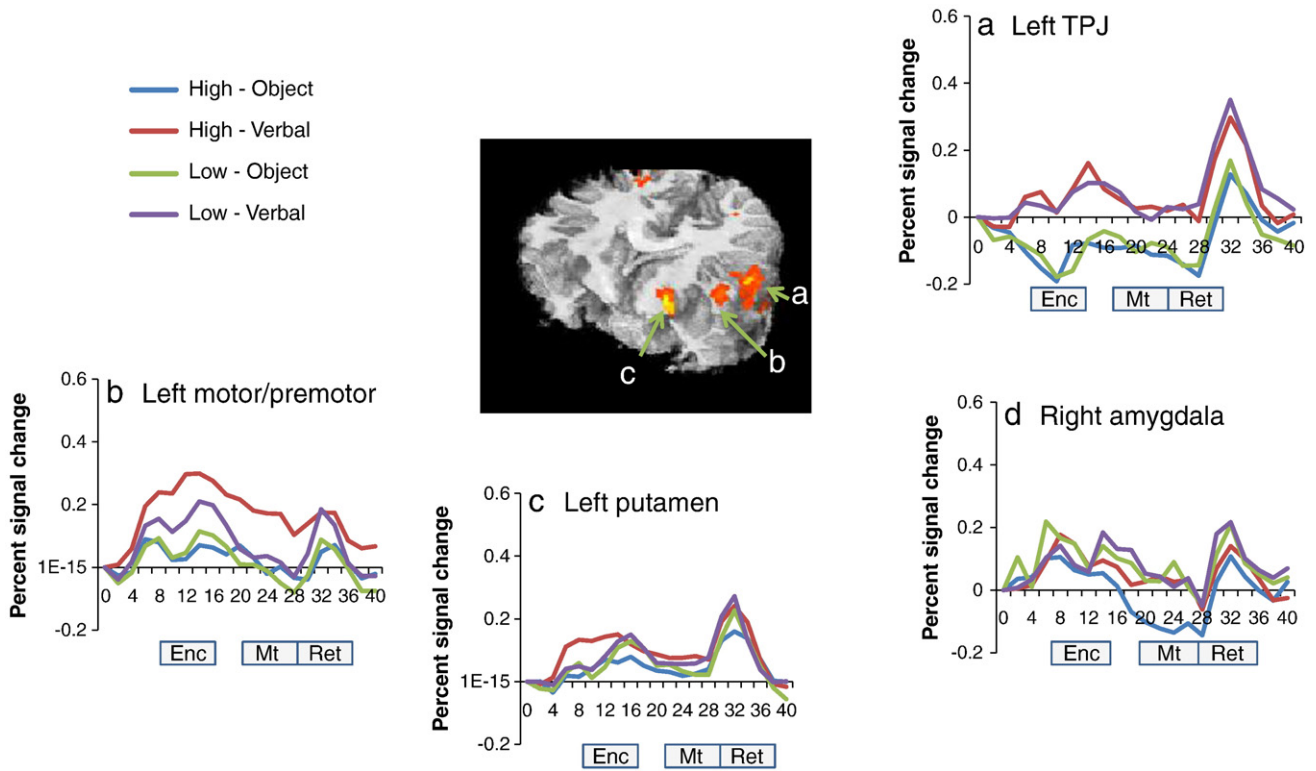


Fig. 5. Time course of regions showing a main effect of information type in the voxel-wise analysis including the a) left TPJ b) left motor/premotor cortex c) left putamen, and d) right amygdala.

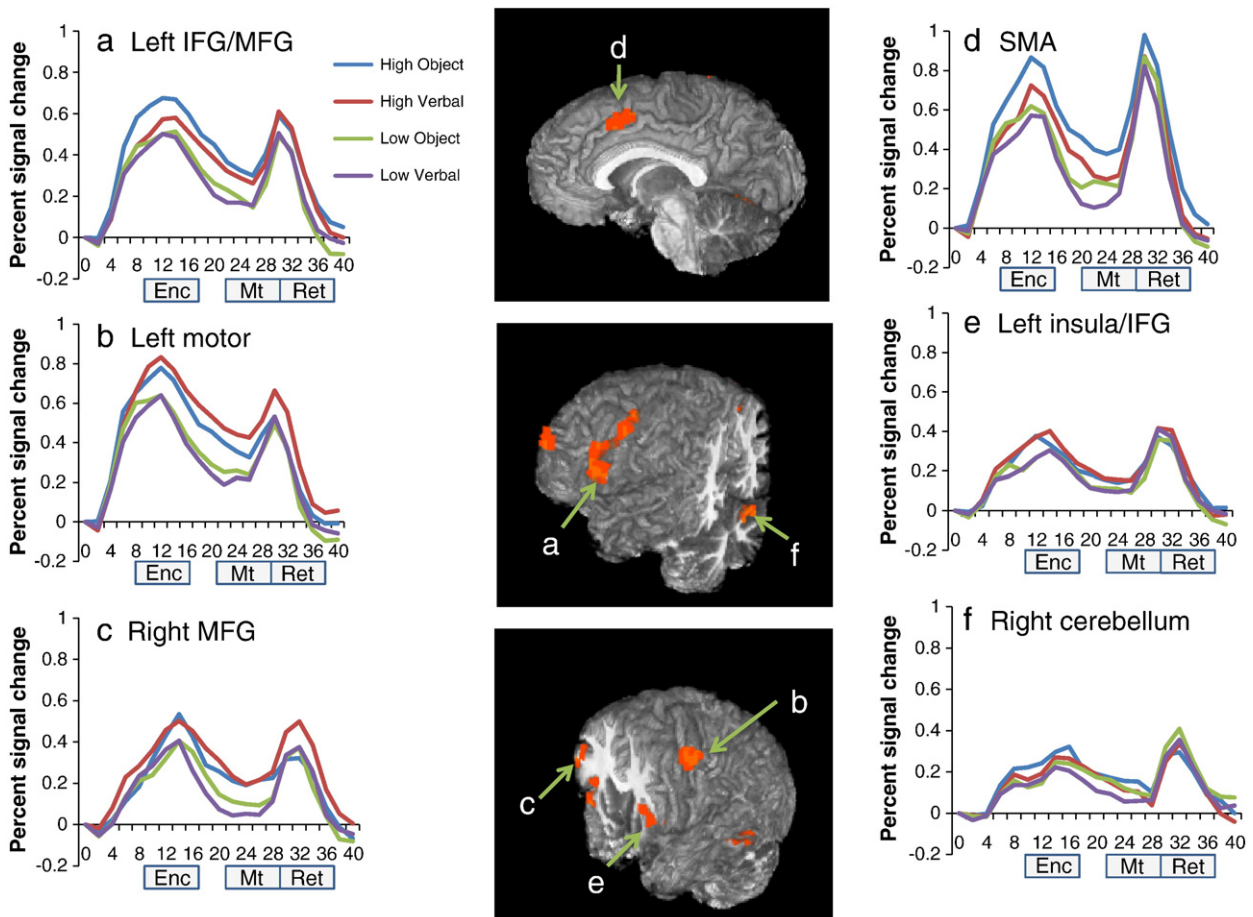


Fig. 6. Time courses of regions showing a main effect of load in the voxel-wise analysis.

verbal stimuli. All these regions demonstrated sustained activity during maintenance in the verbal, high-load condition compared to baseline (left IFG/maintenance ROI: $t(16) = 6.00$, $p < .05$; left IFG/retrieval ROI: $t(16) = 4.10$, $p < .05$; left motor: $t(16) = 4.69$, $p < .05$; SMA: $t(16) = 4.46$, $p < .05$; right MFG, encoding: $t(16) = 3.60$, $p < .05$; right MFG, retrieval: $t(16) = 3.65$, $p < .05$; left insula/IFG: $t(16) = 6.67$, $p < .05$; right cerebellum: $t(16) = 6.20$, $p < .05$). While clearly involved in maintaining information over a delay, these regions are more consistent with domain-general processors involved in central executive processes.

Discussion

A central issue within the WM literature is whether STM processes are independent from processes used to perceive information. Damage to the left TPJ, primarily in the inferior parietal cortex, is associated with deficits in STM capacity without concomitant impairment in speech perception, providing the strongest evidence for the *storage-specific* account of STM (Warrington and Shallice, 1969; Shallice and Vallar, 1990; Vallar and Papagno, 1995). However, activity in this region was not sustained over a delay as would be expected from a short term store. Identical results were obtained using both a pre-specified ROI analysis of the left TPJ and a voxel-wise analysis for regions showing a domain-specific pattern of activity. In contrast, activity in the left STG was more consistent with a region subserving phonological storage. Activity in left STG was domain-specific and was sustained during maintenance. Indeed, activity in the maintenance phase in the left STG was significantly greater than that observed in the left TPJ. Thus, the superior temporal lobe is a much better candidate for maintaining phonological representations than the more parietal TPJ region.

WM storage

Our results suggest that the left posterior STG may be maintaining phonological representations. This region was preferentially active for verbal stimuli and this activity was sustained during the maintenance interval. However, this region has been observed to be involved in speech perception and, thus, does not correspond to a dedicated STM buffer as proposed by the *storage-specific* model. A recent study has shown that patients with lesions to this region have verbal working memory impairments as well as deficits in speech comprehension (Leff et al., 2009). Taken together, these results suggest that the left posterior STG may support speech perception and verbal STM.

Our results are consistent with those reporting delay-specific activity in the left STG (Barch et al., 1996; Buchsbaum et al., 2005; Chein and Fiez, 2001; Chen and Desmond, 2005; Cohen et al., 1997; Fiebach et al., 2006; Hickok et al., 2003; Sakai et al., 2002). Activity over the delay may reflect the re-activation of phonological representations by rehearsal or attentional refreshing. Alternatively, some have argued that this region is important for auditory–motor integration (Hickok and Poeppel, 2000; Hickok et al., 2003). The left STG region assessed in this study is similar to area Spt (Sylvian parietal temporal) thought to be important for integrating both sound- and motor-based phonological representations. Area Spt is located primarily in the temporal lobe (although sometimes activity extends into the parietal cortex) and is more posterior than the left TPJ site, like the STG. According to this proposal, the left STG/area Spt facilitates encoding and rehearsal by integrating articulatory representations that support speech with sound-based phonological representations (Hickok et al., 2003). In a recent study, rTMS directed at the left STG disrupted both verbal working memory and paced reading (Acheson et al., in press). Importantly, auditory–motor integration functions are thought to be important for speech perception, production, and memory (Hickok and Poeppel, 2000).

Thus, *storage-specific* accounts of WM are not supported by activation of a region that is used in speech perception and production.

A clearly-defined STG region was not observed in the voxel-wise ANOVA. One possibility is that STM regions vary more across participants. Postle and colleagues have reported in several studies that posterior regions supporting verbal WM are more variable than prefrontal regions (Feredoes and Postle, 2007; Feredoes et al., 2007; Postle et al., 1999). In these studies, regions supporting STM varied across individuals and included the superior parietal lobe, intraparietal sulcus, the mid precentral gyrus, the STG, the posterior superior temporal sulcus, and the supramarginal gyrus. Note, however, that in our pre-specified ROI analysis, the left TPJ was observed in the voxel-wise tests and was significantly engaged at encoding and retrieval in the group analysis.

Another reason for the lack of the left STG in the whole-brain analysis may have been a tendency to use verbal strategies to remember the Korean letters. This may have led to a weaker difference between verbal and object conditions that would not survive the more rigorous whole-brain threshold of significance. Despite the potential for verbal re-coding, domain specific effects were found at both encoding and retrieval in this region. While the difference between the verbal and object condition was not significant during maintenance, only activity in the verbal conditions was significantly above baseline. Moreover, greater activity was observed in correct verbal conditions compared to errors whereas the opposite was true in the object conditions. The effort of re-coding and remembering the visual match between the Korean letter and the word chosen to represent it may have resulted in an overall decrement in that condition. Indeed, activity in several prefrontal regions was greater for objects than verbal stimuli. In general, it is difficult to find memoranda that cannot be translated into another code (Nystrom et al., 2000), and this may have reduced our ability to find domain-specific effects in this region in a whole-brain analysis.

Neither the left STG nor the TPJ displayed a load effect in our study. This may be due to the manner in which brain activity is assessed in fMRI studies. It is possible that STM activity during maintenance is based on the input from rehearsal regions which will reflect the rate at which items are refreshed in STM rather than reflecting storage capacity. If participants are rehearsing 3 items at the same rate as 5 items, this would negate any load effects in the fMRI signal. As such, differences in rehearsal strategies may determine whether load effects can be observed in storage regions, at least, using fMRI. In contrast, motor, premotor, and prefrontal regions all showed a load effect as would be expected of regions that are driving rehearsal and central executive processes.

Taken together, these results support the idea that regions involved in speech perception and production are maintaining phonological representations in an active state. Although the left TPJ did not fit the criteria of a phonological short-term store, it was engaged in the task at both encoding and retrieval. We propose a novel explanation for this activity in the following section, and suggest that this region is important for implementing attentional capture to verbal stimuli.

The left TPJ – storage or attention?

In the present study, we provide evidence that the pattern of activity in the left TPJ is inconsistent with the profile expected of a storage buffer. Left TPJ activity was not sustained during the maintenance interval and, in fact, was significantly less active during this interval than the left STG. Other studies isolating the maintenance stage have also failed to observe activity in this region during maintenance (Barch et al., 1996; Buchsbaum et al., 2005; Chein and Fiez, 2001; Chen and Desmond, 2005; Cohen et al., 1997; Fiebach et al., 2006; Hickok et al., 2003; Sakai et al., 2002). In contrast, other neural regions including the left STG, the motor/premotor cortex, and

the prefrontal cortex showed sustained activity over the delay (Figs. 5 and 6).

While the left TPJ did not show delay-period activity, significant domain-specific differences were observed between the verbal and nonverbal conditions. Moreover, the left TPJ was recruited during the encoding and retrieval stages of the trial. We suggest that the pattern activity observed in the left TPJ may be consistent with an attentional contribution of this region to WM, and that it may subserve the same function as its homologue in the right hemisphere. This implies that patients with lesions to this area have a reduced verbal WM span because they miss more items at encoding rather than having a reduced ability to store items.

In contrast to the left TPJ's suggested role in verbal STM, the right TPJ is thought to subserve stimulus-driven attention (Corbetta et al., 2008). The right TPJ has been shown in several studies to be responsive to novel or salient stimuli, and is proposed to implement stimulus-driven attentional orienting (Corbetta et al., 2008). In a Posner cuing task, the right TPJ is more active when the target appears, especially when the target is invalidly cued, than during a preparatory interval in which covert attention is directed voluntarily (Corbetta et al., 2000). Moreover, damage to the right TPJ often produces attentional neglect in humans (Mort et al., 2003). It seems possible that the homologous region in the left TPJ functions similarly but shows a preference for speech or speech-like stimuli.

Indeed, both the right and left TPJ are active in imaging studies of oddball detection in which WM demands are low (c.f., Kiehl et al., 2001, 2005; Laurens et al., 2005; Wolf et al., 2008). Oddball detection is considered to be a relatively automatic process similar to pop-out effects in visual search tasks. As such, these tasks are thought to place few demands on WM. We plotted the peak coordinates of left TPJ activity in oddball detection tasks and in verbal WM task. As seen in Fig. 7, the coordinates of peak activity show a high degree of overlap in the left TPJ for studies of oddball detection and verbal WM in spite of the low WM demands in the former task.

In our experiment, stimulus-driven attention should be engaged when stimuli appear (i.e., encoding and retrieval). In contrast,



Fig. 7. Reported peaks of activity in imaging studies of oddball detection (red letters) and verbal working memory (blue letters). Red letters refer to A: Kiehl and Liddle (2001) = $-56, -41, 30$; B: Kiehl et al. (2001) = $-60, -19, 20$; C: Kiehl et al. (2001) = $-44, -34, 25$; D: Kiehl et al. (2005) = $-60, -44, 28$; E: Laurens et al. (2005) = $-64, -36, 20$; F: Laurens et al. (2005) = $-60, -48, 24$; G: Linden et al. (1999) = $-58, -40, 27$; H: Menon et al. (1997) = $-60, -32, 30$; I: Stevens et al. (2000) = $-57, -22, 23$; J: Stevens et al. (2000) = $-59, -49, 23$; K: Stevens et al. (2005) = $-64, -32, 24$; L: Sturm et al. (2004) = $-59, -45, 28$; M: Wolf et al. (2008) = $-62, -28, 18$. Blue letters refer to A: Barch and Csersnansky (2007) = $-62, -22, 24$; B: Gruber and Von Cramon (2001) = $-60, -44, 28$; C: Paulesu et al. (1993) = $-44, -32, 24$; D: Paulesu et al. (1996) = $-44, -34, 24$; E: Ravizza et al. (2004) = $-63, -24, 23$; F: Salmon et al. (1996) = $-56, -22, 24$; G: Salmon et al. (1996) = $-58, -26, 20$; H: current experiment = $-61, -26, 22$.

attention should not be captured during maintenance when items must be covertly rehearsed and stimulus-driven attention could be detrimental. The pattern of left TPJ activity is consistent with a potential contribution to WM by subserving stimulus-driven attention. First, the left TPJ was primarily active when external stimuli were present at encoding and retrieval, but not during maintenance when the task relied on endogenous rehearsal processes. Second, the pattern of activity in this region tended to occur during transition times that may be more likely to capture attention (Pratt and McAuliffe, 2001); namely, activity in this region showed two peaks of activation at the beginning and at the end of stimulus presentation. While not conclusive, these results suggest that the left TPJ may facilitate attentional orienting to verbal stimuli.

While the claim that the left TPJ is serving an attentional role is novel, the right TPJ has long been thought to be important for stimulus-driven attention. Numerous studies by Corbetta, Shulman, and colleagues have shown a strong association between stimulus-driven attention and the right TPJ. Thus, it would be informative to determine how a region more robustly linked to attention responds in our WM task. We examined the time course of activity in the right TPJ by creating a mask of the homologous region to the left TPJ. Similar to the left TPJ, activity during maintenance was no different from baseline activity ($p > .1$) (see Fig. 8). Moreover, it also displayed greater activity during the offset and onset of external stimuli.

Anticevic et al. (2009) assessed activity in the right TPJ and found that this region was suppressed during encoding into visual WM. In this previous study, several types of distracters were presented during the maintenance interval that participants were required to ignore. In our study, no distracters were presented making it unlikely that attention would be captured by irrelevant stimuli. We speculate that both the left and right TPJ would be suppressed if distracters had been presented in our study to prevent irrelevant information from disturbing the contents of WM. However, this idea needs to be tested in future studies.

The left TPJ was more responsive during retrieval compared to encoding and maintenance. This pattern of response does not fit the assumptions of a short term store, but may fit the attention hypothesis proposed here. It is possible that endogenously-driven or voluntary attention was used during the maintenance period to help maintain items in WM as suggested by Cowan (1995). If so, stimulus-driven attention may have been critical for detecting the probe given that endogenous attentional resources were recruited for maintenance. The greater activity for the verbal conditions at retrieval suggests that the left TPJ may orient attention preferentially to verbal stimuli. Alternatively, the left TPJ may be important for the act of retrieving rather than directing stimulus-driven attention to the probe. The current data do not allow us to distinguish between these two accounts, but both posit a role for the TPJ that is separate from storage.

Conclusion

In sum, our data do not support the existence of a separate storage buffer uninvolved in speech perception. Originally, this argument was premised on the fact that left TPJ lesions were associated with reduced verbal span but preserved speech perception. However, this region does not respond in a way predicted by a short-term store in our fMRI study. Our data are more consistent with the idea that primary and secondary auditory and motor cortices maintain this information as reported in studies of visual WM (Serences et al., 2009). Thus, we find little support for the separation of perceptual and STM processes. Instead, we find evidence that verbal information is maintained in systems that are used to perceive such information. While damage to the left TPJ is associated with low verbal WM spans, we suggest that this region facilitates verbal encoding by orienting attention when such information is presented. Our findings highlight a potential role of attentional capture to successful verbal maintenance.

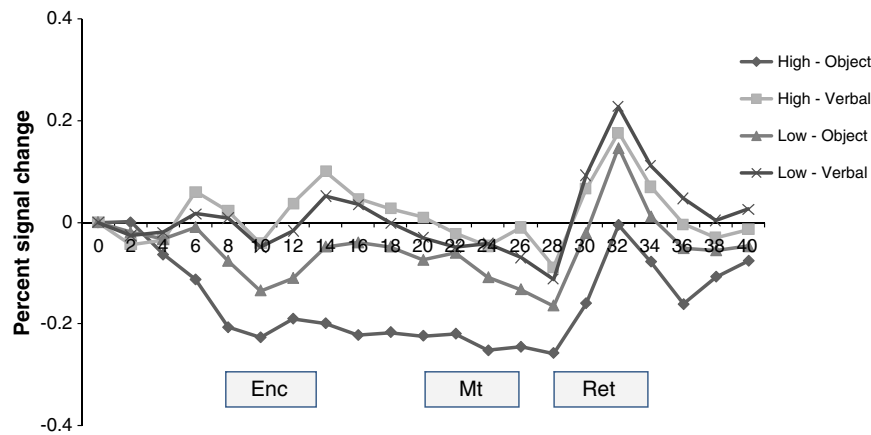


Fig. 8. Time course of activity in a pre-specified ROI in the right TPJ.

Acknowledgments

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Appendix A. Supplementary data

Supplementary data to this article can be found online at doi:10.1016/j.neuroimage.2010.12.021.

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