Functional dissociations within the inferior parietal cortex in verbal working memory

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Neuroimaging studies of working memory have revealed two sites in the left supramarginal gyrus that may support the short-term storage of phonological information. Activation in the left dorsal aspect of the inferior parietal cortex (DIPC) has been observed in contrasts of working memory load, whereas activation in the ventral aspect of the inferior parietal cortex (VIPC) has been found primarily in contrast of information type (verbal vs. nonverbal). Our goal was to determine whether these two areas are functionally distinct or if instead they are part of a homogeneous region with large variations in the focus of peak activity. Toward this end, we used fMRI to assess the neural response in two working memory tasks (N-back and item recognition) in which we also manipulated memory load and the type of information to be recalled (verbal vs. nonverbal). We found both DIPC and VIPC activation in the same group of subjects and further demonstrated that they have differential sensitivity to our experimental factors. Only the DIPC showed robust load effects, whereas only the VIPC showed reliable effects of information type. These results help to account for the differences observed in between-subject comparisons, and they indicate that the two regions are functionally dissociable. In contrast to the DIPC, activity of the VIPC was also recruited in the fixation and low-load conditions, a surprising result that has not been fully explored in prior studies. Despite their distinctive patterns of performance, neither of these regions displayed a pattern of activity that entirely corresponds to common assumptions of a dedicated phonological short-term store (STS). Instead, we hypothesize that the DIPC may support domain-general executive processes, while the VIPC may support phonological encoding–recoding processes central to a variety of language tasks.
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According to one influential model of working memory (Baddeley and Hitch, 1974), the ability to remember verbal information for a brief time is contingent upon a system dedicated to the storage of phonological material. Verbal items (e.g., digits, letters, or words) are maintained in this store and are periodically refreshed by articulatory rehearsal to prevent their rapid decay. Auditory information is claimed to have obligatory access to this dedicated linguistic short-term store (STS), although visually presented items can also be maintained through this route if they are phonologically recoded. However, the STS is claimed to be a separate system from that used for phonological perception (Baddeley et al., 1998; Martin and Breedin, 1992).

The primary evidence for a distinct phonological store and perceptual system includes several accounts of patients with reduced spans for verbal information without a concomitant deficit in the identification or discrimination of phonemes (Vallar and Baddelely, 1984; Warrington and Shallice, 1969). Research with these patients has also suggested that the STS is specialized for linguistic material as these patients have no difficulty with visuo-spatial working memory tasks (Shallice and Warrington, 1974; Vallar and Papagno, 1995). Their pattern of deficit, then, suggests a neural area that is dedicated to the storage of verbal material but is not involved in the initial perception of the items to be remembered. The left temporoparietal junction has been suggested as the anatomic substrate of such a store, as it is the most commonly reported lesion site for patients with a selective deficit of verbal working memory (Shallice and Vallar, 1990).

Imaging studies of verbal working memory have attempted to localize the site of the phonological store more precisely (e.g., Paulesu et al., 1993; Smith et al., 1996). However, two distinct regions of the supramarginal gyrus are claimed to function as the phonological STS (Becker et al., 1999)—a region of the inferior parietal cortex with a more dorsal focus [dorsal aspect of the inferior parietal cortex (DIPC)] and a region with a more ventral focus [ventral aspect of the inferior parietal cortex (VIPC)] near the site associated with short-term memory deficits in patients. While these regions are often considered to function homogenously

(Bunge et al., 2000; Cabeza et al., 2002; Clark et al., 2000; Henson et al., 2000; Tsukiura et al., 2001), one way to reconcile the paradoxical neuroimaging and neuropsychological findings is to propose that these regions make different contributions to verbal working memory tasks.

For instance, most studies reporting DIPC activity have contrasted memory load (e.g., delay interval, number of items), whereas studies reporting VIPC activity have contrasted verbal and nonverbal working memory conditions. These findings suggest that the DIPC is recruited in memory-intensive conditions when attentional demands are high. On the other hand, the VIPC appears to be selectively active for verbal material regardless of memory load. To test these accounts of DIPC and VIPC activation, load and information type (verbal–nonverbal) were manipulated in a single scanning session; this allowed us to determine whether both DIPC and VIPC foci of activation could be found within the same group of subjects and, if so, whether these regions showed functionally distinct patterns of activation. Based upon prior observations of inferior parietal activity during verbal working memory tasks, we hypothesize that the DIPC and VIPC are functionally dissociable, with the DIPC demonstrating sensitivity to load but not information type and the VIPC showing sensitivity to information type but not load.

More specifically, performance on two working memory tasks that have been previously associated with parietal activation were compared. The N-back task was employed, because it has evoked robust activity of the DIPC in previous studies (Cohen et al., 1997; D'Esposito et al., 1998; Jonides et al., 1997). Given that the majority of the working memory studies reporting VIPC activity have used an item-recognition paradigm, participants were tested on this task as well. Moreover, both load (high or low) and information type (verbal or nonverbal) were manipulated in these working memory tasks to assess inferior parietal activity across the entire set of conditions. For the verbal versus nonverbal contrast, English and Korean letters were used as stimuli, since prior studies have shown greater VIPC activation for English versus Korean letters (Paulesu et al., 1993, 1996; Salmon et al., 1996).

If the DIPC and VIPC display the response we have predicted to manipulations of load and information type, their suitability as the locus of the STS is in question. Based upon Baddeley's model of verbal working memory, the phonological store might be expected to show both effects of load (since more information would need to be encoded and maintained in the store as the load is increased) and effects of item type (since the store is thought to be specifically dedicated to the maintenance of verbal information). More precisely, a within-subjects design should reveal an interaction between load and information type in a region that functions as a dedicated phonological short-term store, with robust activation for the verbal high-load condition and low activation for all other conditions. Thus, if our hypothesis is upheld, it would suggest that neither the DIPC nor the VIPC exhibits a pattern of activity consistent with current conceptions of phonological storage and that alternative interpretations of both DIPC and VIPC function should be considered.

Experiment

To increase the reliability of our results, we tested two separate groups of participants using either a 1.5- or a 3-Tesla (T) magnet on identical tasks. Our first aim was to replicate previous reports of

DIPC and VIPC activity using simple load or information-type contrasts. Toward this end, we examined parietal activity by observing load effects in the verbal condition alone, in line with previous verbal working memory studies (Cohen et al., 1997; D'Esposito et al., 1998; Jonides et al., 1997). Moreover, to replicate previous information type effects (Paulesu et al., 1993, 1996; Salmon et al., 1996), we assessed whether parietal activity was greater in the verbal than the nonverbal, high-load condition. In the next section, we determined whether either parietal region displayed the interaction effect that we argue is predicted for a phonological store by the Baddeley model. Finally, we examined parietal regions that exhibited a load effect in the nonverbal memory task to assess whether these areas were selective for verbal items.

Methods

Participants

Twenty-one right-handed adults (10 male, 11 female) with ages ranging from 18 to 37 were paid US$46 to participate in this experiment (1.5 T: $n = 10$; 3 T: $n = 11$). All provided informed consent following procedures approved by the Institutional Review Board at the University of Pittsburgh. One participant's N-back data had to be excluded due to poor task compliance.

Stimuli

The verbal stimuli consisted 18 English letters (B, C, D, F, G, H, J, K, M, N, P, Q, R, S, T, V, X, and Z). A set of 18 Korean letters that looked least like English letters (a, chiuch, hiuh, i, iung, khukh, kiyek, mium, niun, o, ou, phuph, piup, sios, tikut, xpiup, xsios, and ye) comprised the nonverbal set (see Fig. 1). All of the participants confirmed that they could not read Korean.

Procedure

The experiment was identical regardless of the scanner used to collect images. Versions of the N-back and item-recognition tasks were created to manipulate both load and information type. Thus, for each task, there were four conditions—high-load verbal, low-load verbal, high-, and low-load nonverbal (see Figs. 1 and 2). For the N-back task, items were presented every 3 s. In the low-load version of the N-back (0-back) task, participants were asked to press a button with their right index finger if a specific target appeared. The target was the letter "X" in verbal blocks and was the Korean letter "sios" in the nonverbal conditions. If any other item besides the target appeared on the screen, participants were asked to press a button with their right middle finger. In the high-load version of the N-back task (3-back), participants determined whether an item was the same as one at three trials back. If the item was the same, participants pressed the button under their right index finger. Participants pressed the button under their right middle finger if the item was different than the one presented three trials back. In the verbal 3-back task, participants were encouraged to rehearse the letters presented in the last three trials while continuously updating their list as each new letter appeared. Items were visible for 500 ms and were followed by a fixation cross that appeared for 2500 ms. Twelve items were presented in each block of trials, so that each block lasted 36 s. The probability of an item
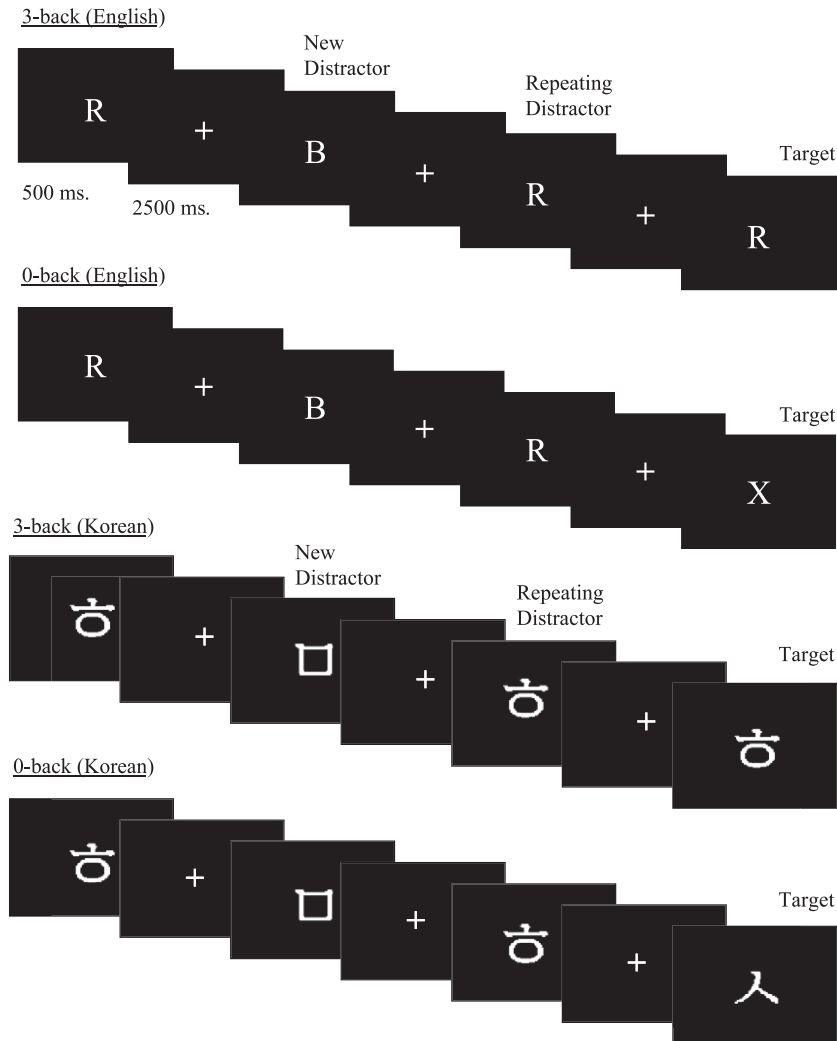
Fig. 1. Examples of the 0- and 3-back tasks for both the English and Korean conditions in the *N*-back paradigm.

being a target was 33%, whereas new distracters and repeated distracters appeared 47% and 20% of the time, respectively.

The item-recognition task began with the serial presentation of six items followed by a short delay and then the presentation of a probe item (see Fig. 2). Each item was visible for 500 ms, after which a fixation cross would appear for 500 ms. After the set of six items had been presented, a short delay of 2000 ms occurred and was succeeded by the appearance of a probe item for another 2000 ms. In the low-load condition (detect), participants determined whether a specific target had been in the list of six items. The probe was the same as those used in the 0-back task described previously (i.e., "X" or "sios"). Conversely, participants were unaware of what the probe item would be in the high-load version of the task (rehearse) and were encouraged to rehearse the set of six letters in the English condition. The probability that the subsequent probe matched one of the six items in the list was 50%. Items that matched the probes could be presented in any portion of the list in the rehearse condition, while in the detect condition, they were weighted to occur more frequently in the final three items to increase the likelihood that participants would pay attention to the entire set of items. Participants pressed a button with their index finger if the probe item matched one of the six

items on the list or a button with their middle finger if it did not. Five lists were presented in a block of trials, and each block lasted 56 s.

Each participant in the scanner performed five runs of both the *N*-back and item-recognition tasks. A run was composed of five blocks—each combination of the English or Korean and high- or low-load conditions and one fixation control block. For the fixation block, participants were instructed to fixate on the cross presented in the center of the screen. The probability of a run beginning with the English or Korean conditions was 50%. Load was counterbalanced across participants so that half began each run with the low-load conditions and half began with the high-load conditions. The fixation block was always the third block in the run. Thus, a run for the *N*-back task might be (1) Korean–0-back, (2) Korean–3-back, (3) Fixation, (4) English–0-back, or (5) English–3-back. All participants received one training block on both working memory tasks before being scanned.

Functional MRI protocol

Ten participants performed the experiment in a 1.5-T GE Signa scanner. The scanning session began by obtaining 30 T1-weighted
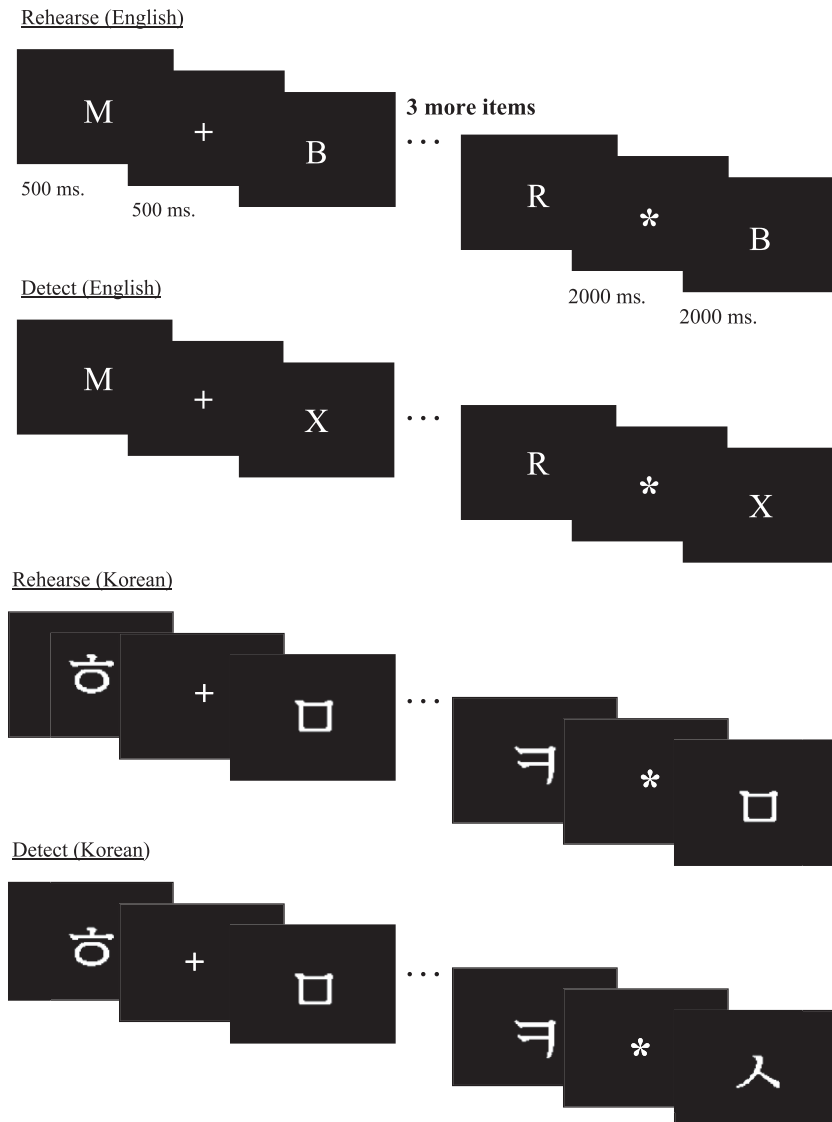
Rehearse (English)

Detect (English)

Rehearse (Korean)

Detect (Korean)

Fig. 2. Examples of the detect and rehearse tasks for both the English and Korean conditions in the item-recognition paradigm.

images for anatomical localization (0.9375 × 0.9375 × 3.8 mm). Participants then performed the experiment while T2*-weighted gradient echo, 1-shot spiral scans were acquired parallel to the AC–PC line. Twenty-six 3.8-mm, contiguous oblique-axial slices were obtained every 2 s with each voxel having an in-plane resolution of 3.75 × 3.75 mm. (TR = 2 s; TE = 35 ms; flip angle = 70°). Functional images were acquired in the same plane as the anatomical scans, but coverage was limited to the top 26 slices— extending from superior portions of the cortex to more superior regions of the cerebellum. This protocol permitted us to acquire 90 and 140 volumes for each of the five conditions in the N-back task and item-recognition tasks, respectively.

Eleven participants performed the experiment in a 3-T GE Signa scanner. The scanning session began by obtaining 36 T1-weighted images for anatomical localization (0.78125 × 0.78125 × 3.2 mm). Acquisition was identical to that reported for the 1.5-T magnet (1-shot, spiral scans; see above), except that thirty-six 3.2-mm slices were obtained with each voxel having a resolution of 3.125 × 3.125 mm. (TR = 2 s; TE = 18 ms; flip angle = 80°).

Images were first corrected for motion using a six-parameter rigid-body automated image registration (AIR) algorithm and then detrended with a linear regression to remove scanner drift. We chose one participant's structural scans from each scanner group to serve as a common reference brain that was then used to coregister all participants' structural and functional images within that group. These reference brains were also transformed into Talairach space using the AFNI program (Cox, 1996). To minimize differences in intensity between participants, functional images were normalized by scaling each image to a global mean intensity. These images were then smoothed using an 8-mm full-width, half-maximum Gaussian kernel to reduce anatomical differences between subjects.

Functional MRI data analysis

All ANOVAs were computed using the Neuroimaging Software package (NIS 3.5;, http://kraepelin.wpic.pitt.edu/nis/) developed at the University of Pittsburgh and Princeton University. The images acquired for each participant in each condition were first

averaged and then subjected to the ANOVA program that generated spatial F-maps. By averaging images across participants, we were able to determine reliable areas of activity within the group while discounting individual differences in functional anatomy. Given that we were using coordinates averaged across multiple studies to define the VIPC and DIPC, it was more appropriate to analyze the group data to compare our results with previous studies. For these tests, subject was designated as a random factor. Moreover, ROIs had to survive a threshold of $P < 0.005$ and consist at least four contiguous pixels to be considered a source of significant activation. Main and interaction effects were assessed using a critical F value of 13.61 [$F(1,9) = 13.61$, $P < 0.005$]. If post hoc tests were necessary to determine significance between multiple variables, a t test was performed using the mean intensity values for each participant in a given condition for a particular ROI.

It is important to note that our threshold in the voxelwise test results in a mapwise false-positive rate that exceeds 0.05 across the entire set of brain voxels. However, the primary aim of these tests was to serve as a method of localization for our a priori regions of interest so that we could explore the pattern of parietal, frontal, and cerebellar activity across the full set of conditions. By using functionally defined regions rather than predefined ROIs based on previous literature, we ensure that the maximally affected voxels lie within a given area. Moreover, as we predicted that some regions would not be modulated by certain manipulations (e.g., DIPC should not show an effect of information type), we felt that a more liberal criterion would actually serve as a more conservative test of our predictions.

Voxelwise tests

To compare our results to previous verbal working memory studies, we began by performing the analyses typically used in these studies. Thus, we performed separate load and information type voxelwise ANOVAs for the N-back and item-recognition tasks to see if we could replicate load effects in the DIPC and information type effects in the VIPC.

A region was considered part of the DIPC if its peak was centered in the x and y dimension ± 1.5 cm (approximately 2 SD) away from mean coordinates ($x = -34$, $y = -51$) derived from 23 studies of working memory (Awh et al., 1996; Barch et al., 1997; Braver et al., 1997; Bunge et al., 2000; Callicott et al., 1999; Chein and Fiez, 2001; Clark et al., 2000; Cohen et al., 1997; Coull et al., 1996; Davachi et al., 2001; D'Esposito et al., 1998; de Zubicaray et al., 1998; Henson et al., 2000; Jonides et al., 1997, 2000; Marshuetz et al., 2000; Petrides et al., 1993; Reuter-Lorenz et al., 2000; Rypma et al., 1999; Salmon et al., 1996; Schumacher et al., 1996; Smith et al., 1996; Tsukiura et al., 2001). Moreover, the peak had to fall within the range $z = 32$ to 52 mm reported in previous studies. To be considered part of the VIPC, the peak activity had to be within ± 1.5 cm of the x and y dimensions ($x = -52$ mm, $y = -27$ mm) obtained from averaging coordinates across studies reporting VIPC activity (Becker et al., 1996; Paulesu et al., 1993, 1996; Salmon et al., 1996) and also fall within the range of $z = 10$ to 30 mm. Although inferior parietal cortex ends at approximately $z = 14$ mm, we considered that the VIPC and portions of the superior temporal gyrus may not be functionally distinct given that short-term memory patients have lesions that encompass the temporoparietal junction. Furthermore, this range more closely approximates the height criteria used to define areas of the DIPC.

ROI analyses

To determine the full pattern of load and information type effects, we then selected a subset of the general areas identified by these voxelwise ANOVAs for further analysis. The selected areas consisted of our a priori regions of interest in parietal cortex (DIPC and VIPC) and a set of comparative areas previously associated with the specific rehearsal of verbal information [left Broca's area (BA), the SMA, and the cerebellum] and general executive processing (left DLPFC and right DIPC).

Our goal was to determine the typical pattern of activity across conditions, regardless of task, statistical contrast, magnet (1.5 or 3 T), or precise location of the peak of activation. For each general area of interest, there were potentially eight contributory locations within a given region found in our first analysis step: the specific regions of significant activation found in our contrasts of load in the N-back task, information type in the N-back task, load in the item-recognition task, and information type in the item-recognition task for participants scanned in the 1.5- and 3-T scanners. In cases where multiple regions of activation were found in a single area for a given contrast and group (e.g., the two left DIPC regions in the contrast of load in the item-recognition task for participants in the 3-T group), we selected the region that was closest to the center of the search criteria for our two parietal regions or (for areas outside of the parietal lobe) the region that was most consistent with the peak coordinates obtained across other contrasts in our data. First, we averaged the data produced by each group in each region, combining the data from the first subject scanned in the 1.5- and 3-T magnets, the data from the second subject scanned in the 1.5- and 3-T magnets, and so forth. After averaging across magnets, we averaged the signal values obtained from locations within each region that was identified by the load and information contrasts for the N-back task, and we averaged the signal values obtained in the load and information-type contrasts for the item-recognition task. Finally, the averaged values for each task were averaged together to obtain one set of values in each condition. The resulting set of signal values was then analyzed using an ANOVA with load and information type as factors, for each of our six general areas of interest (left VIPC, left DIPC, right DIPC, left DLPFC, SMA, left Broca's area, and left and right cerebellum).

Results and discussion

Given that the procedure was identical for both groups (1.5 and 3 T), they are discussed in the same section, although the results are reported separately for each magnet in the tables.

Behavioral data

Participants' accuracy in each task was analyzed using a $2 \times 2 \times 2 \times 2$ (task × load × information type × magnet) repeated-measures ANOVA. Main effects for load [$F(1,18) = 195.23$, $P < 0.001$] and information type [$F(1,18) = 23.68$, $P < 0.001$] were obtained, as well as the interaction effect of these two variables [$F(1,18) = 15.19$, $P < 0.001$] (see Fig. 3). An analysis of simple effects confirmed that the difference between the English and Korean high-load conditions was significant [$t(19) = 4.56$, $P < 0.001$], whereas the difference between the low-load conditions was not ($P > 0.1$). Furthermore, participants were slightly less accurate in the item-recognition task in general than the N-back task (92% vs. 93%), although the effect was not significant
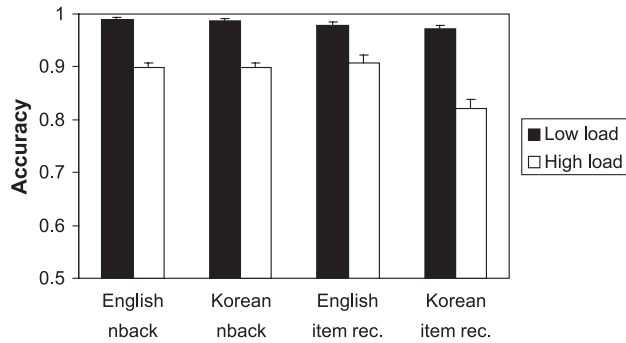
Fig. 3. Accuracy in the N-back and item-recognition tasks for Groups 1 and 2.

$[F(1,18) = 3.16, P = 0.093]$. Neither a main effect of magnet nor an interaction of magnet with any other variable was obtained.

The fact that participants were more accurate in the low-load conditions confirmed that our load manipulation was effective in increasing task difficulty. Moreover, the difference in accuracy between the English and Korean conditions indicates that participants were using a less effective strategy to perform the task when having to remember Korean letters. Although it is possible to verbally encode Korean letters (e.g., "ring," "lambda"), the ease of encoding English letters provided an advantage for the verbal items that were especially apparent in the high-load conditions.

Imaging data—N-back

Studies reporting DIPC activity have typically compared verbal high- and low-load conditions. Thus, we subjected the imaging data from both magnets to separate repeated-measures ANOVAs using mean intensity values from the English 3- and 0-back conditions. As expected, in the 1.5-T group, a number of regions were affected by load (see Table 1), including areas generally associated with central executive processes (e.g., dorsolateral prefrontal cortex) and articulatory rehearsal (e.g., the supplementary motor area, the left premotor cortex, Broca's area, and the cerebellum). Note that the DIPC, but not the VIPC, was significantly active in this load contrast—a result in line with previous N-back experiments. Moreover, these results were replicated by the participants scanned in the 3-T magnet. The DIPC was active in both studies regardless of the magnet used, whereas VIPC activity was not detected by a load contrast for either group.

In contrast, VIPC activity is usually reported when verbal and nonverbal high-load conditions are compared. When we compared the English and Korean 3-back tasks in repeated-measures ANOVAs, we found both DIPC and VIPC activities for participants scanned with the 1.5-T magnet, but only VIPC activity for those scanned with the 3-T magnet (see Table 2). Thus, the VIPC, but not the DIPC, displayed robust effects of information type.

Imaging data—item recognition

To assess load effects for this task, we compared scans acquired in the English rehearse (high-load) condition to those in the English detect condition (low-load). Neither parietal region was active in this contrast, and concerned that our low-load condition placed an observable demand on memory, we additionally compared the English rehearse task to the fixation control condition. For both experiments, DIPC was recruited more heavily in the high-load condition than in the fixation condition. In contrast, the VIPC was

Table 1
Neural regions showing a consistent effect of load in the English conditions ($P < 0.005$)

Region	BA	N-back 1.5 T			N-back 3 T			Item recognition 1.5 T			Item recognition 3 T		
		x	y	z	x	y	z	x	y	z	x	y	z
SMA/anterior cingulate	6/32	2	19	48	6	17	46	0	1	56	−1	2	49
								−4	−4	66			
								−1	−15	43	9	11	37
Left premotor cortex	6	−29	−3	56	−23	−2	50	−32	−7	43	−25	0	47
Right premotor cortex	6	31	5	58	27	−1	45	29	1	59	29	−1	42
					47	−2	37	44	−1	36			
Left DLPFC	9/10/46	−39	23	36									
		−33	46	28	−30	47	17				−34	32	20
Right DLPFC	9/46	46	8	39	43	19	40	38	30	36	46	30	27
		40	35	33	34	32	22						
Left premotor/Broca's area	6/44/45	−46	7	34	−41	17	36				−39	3	25
Right premotor/VLPFC	6/44/45							33	21	13	46	1	33
Right insula		34	23	7							38	18	1
Right posterior parietal	7				42	−71	43	30	−67	45			
Left DIPC	40	−42	−47	38	−47	−55	44	−24	−61	37	−37	−42	37
											−26	−61	35
Right DIPC	40	48	−51	40	46	−48	42				40	−44	39
Left VIPC													
Left caudate								−8	−7	22	−18	−8	22
											−26	−31	22
Right caudate								18	5	20	15	−9	20
Left cerebellum					−23	−58	−29				−40	−58	−24
					−31	−41	−31						
Right cerebellum					30	−61	−28	46	−50	−19	35	−60	−21

Except for the inferior parietal cortex, only regions that were active in two of four experiments are listed.

Table 2
Neural regions in Experiments 1 and 2 showing an effect of information type in the high-load conditions ($P < 0.005$)

Region	BA	N-back						Item recognition					
		1.5 T			3 T			1.5 T			3 T		
		x	y	z	x	y	z	x	y	z	x	y	z
SMA/anterior cingulate	6/32				3	8	50			3		−7	45
Left premotor cortex	6	−43	−5	48	−47	−4	57						
Right premotor cortex	6	31	7	52	29	11	50						
Right ventral prefrontal	44/45	63	5	28	33	14	15			45		5	7
Left DIPC	40	−27	−41	36									
		−44	−40	35									
Left VIPC/STG	40/22	−63	−24	23	−65	−34	12				−63	−30	−10
Left cerebellum					−26	−59	−27				−41	−67	−42

Except for the inferior parietal cortex, only regions that were active in two of four experiments are listed.

not apparent using a load contrast. Thus, the DIPC displayed load effects in both the N-back and item-recognition paradigms, whereas the VIPC was not affected by load in either task.

Information type effects (verbal vs. nonverbal) in the item-recognition task were examined by a repeated-measures ANOVA using scans acquired in the English and Korean rehearse conditions. For those scanned with the 1.5-T magnet, we were unable to find inferior parietal involvement or indeed any neural activity that was greater in the English condition in our voxelwise analyses. For the 3-T group, a region of the VIPC/superior temporal gyrus displayed greater activity in the English than in the Korean conditions. Thus, in both memory paradigms, the VIPC was engaged by verbal stimuli, whereas the DIPC displayed less robust effects of the type of information to be remembered.

The null result of information type for images acquired in the 1.5-T magnet is somewhat surprising given that our version of the item-recognition task was almost identical to those used in previous studies of working memory for English and Korean letters. One important difference between the studies reporting VIPC involvement and the experiment reported here is the methodology used to image neural activity. Our experiment implemented fMRI to explore verbal working memory effects, while previous studies finding VIPC activity have all used PET (Becker et al., 1996; Paulesu et al., 1993, 1996; Salmon et al., 1996). PET imaging differs from fMRI in ways that may produce differences in sensitivity to neural activity, especially in high-order linguistic tasks (Veltman et al., 2000), and so a small difference between the English and Korean conditions may be less detectable using fMRI than PET. Although the timing of acquisition was identical for both scanners, boosting the signal strength may have allowed us to detect responses with the 3-T magnet in the item-recognition task, which were below our statistical threshold with the 1.5-T magnet.

Interaction effects across tasks

A simple prediction of the Baddeley model is that regions selectively involved in either articulatory rehearsal or phonological storage should be affected by the interaction of load and type of information, with robust activation observed only in the verbal high-load condition. Specifically, markers of storage and rehearsal should display greater activity in the English high-load conditions (i.e., 3-back, rehearse) than in all the other conditions. Of interest is the pattern of activity of six regions previously associated with either phonological storage (i.e., left DIPC, left VIPC) or the

articulatory loop (e.g., Broca's area, SMA, and bilateral cerebellum). Moreover, we wanted to assess the pattern of activity of the right homologue of the left DIPC. Activity of the right DIPC was observed in this and other verbal working memory experiments (Cohen et al., 1997; Henson et al., 2000; Jonides et al., 1997; Tsukiura et al., 2001) and may be part of a general attentional network (Chein et al., in press; Corbetta et al., 2000; Wojciulik and Kanwisher, 1999). Activity of an additional executive region, the left DLPFC, was also observed across conditions. Like the left DIPC, the left DLPFC is often reported in both verbal and spatial working memory studies but has been claimed to be more important for remembering verbal items (Reuter-Lorenz et al., 2000; Smith et al., 1996; although see D'Esposito et al., 1998).

Regions associated with articulatory rehearsal displayed a significant interaction effect [Broca's area: $F(1,9) = 9.06$, $P < 0.05$; SMA: $F(1,9) = 30.44$, $P < 0.001$; right cerebellar cortex: $F(1,9) = 9.98$, $P < 0.05$; left cerebellar cortex: $F(1,9) = 8.02$, $P < 0.05$] (see Fig. 4 for a subset of these areas). All of these regions displayed the same pattern of results; that is, they were recruited more heavily in the English high-load condition than all three other conditions (all $Ps < 0.05$). Thus, neural markers of articulatory rehearsal performed in a way consistent with Baddeley's model.

The VIPC also displayed a significant interaction effect [$F(1,9) = 26.15$, $P < 0.001$] but did not behave as would be predicted of a phonological short-term store. Although activity was greater in the verbal high-load condition than the nonverbal [$t(9) = 8.42$, $P < 0.001$], this area showed no effect of load in the verbal conditions. A neural substrate of the short-term store should show a load effect given that the area would be periodically refreshed by the rehearsal system in the high-load but not the low-load condition. Moreover, this area was just as active in conditions that place little demand on working memory (i.e., the fixation and Korean low-load conditions) as in the memory-intensive verbal condition. In contrast to rehearsal areas, the VIPC did not behave in a way that corresponds to current notions of the phonological short-term store.

The DIPC fares no better in this regard. This area did not display an interaction effect of load and information type [$F(1,9) = 3.08$, $P = 0.113$] and exhibited only a marginal effect of information type [$F(1,9) = 4.92$, $P = 0.054$]. However, a main effect of load was obtained [$F(1,9) = 44.32$, $P < 0.001$]. The DIPC was primarily recruited when load was heavy regardless of the linguistic nature of the items to be remembered. In fact, this region tended to be more or equally active in the Korean high-load than the English high-load condition in the item-recognition task [1.5 T: English (Eng) =
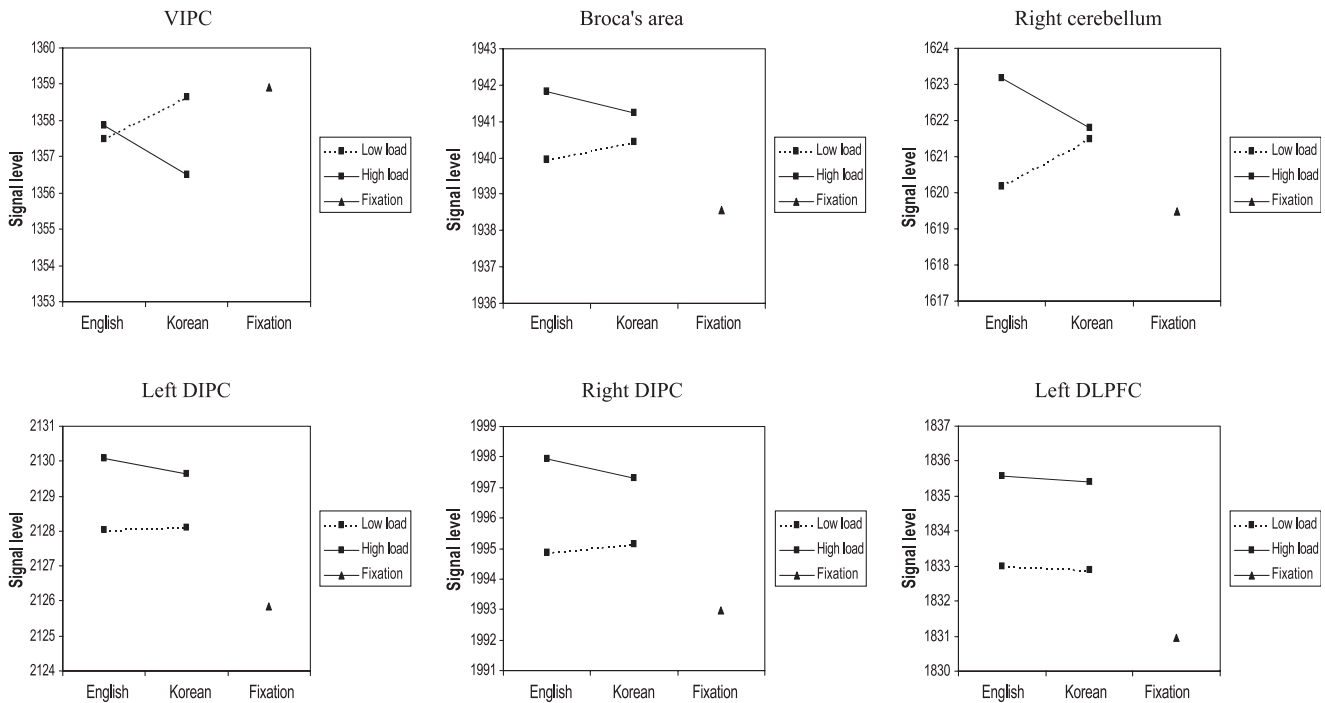
Fig. 4. Overall pattern of activity across the entire set of conditions for the VIPC, Broca's area, the right cerebellum, the left and right DIPC, and left DLPFC.

2189.97, Korean (Kor) = 2190.32; 3 T: Eng = 2224.31, Kor = 2224.42]. Moreover, the DIPC displayed the same pattern of activity across conditions as the two attentional–executive regions—the right DIPC and left DLPFC. Neither of these latter regions showed a significant interaction effect [rDIPC: $F(1,9) = 3.88$, $P = 0.08$; lDLPFC: $F(1,9) = 0.02$, $P = 0.889$], but both were recruited when load was high regardless of information type [rDIPC: $F(1,9) = 44.98$, $P < 0.001$; lDLPFC: $F(1,9) = 47.7$, $P < 0.001$].

To assess whether the VIPC and DIPC were functionally distinct, we directly compared signal levels from these regions in a 2 (area) × 2 (load) × 2 (information type) ANOVA. The three-way interaction was significant [$F(1,9) = 17.24$, $P < 0.005$]. Paired-sample t tests using the difference scores demonstrated that (a) there was a greater difference between the English high- and low-load condition in the DIPC than the VIPC [$t(9) = 2.4$, $P < 0.05$], (b) the difference between the Korean high- than low-load conditions was positive for the DIPC and negative for the VIPC [$t(9) = 7.96$, $P < 0.001$], (c) there was less of a difference between the English and Korean high-load conditions in the DIPC than the VIPC [$t(9) = 4.1$, $P < 0.005$], and (d) there was less of a difference between the English and Korean low-load conditions in the DIPC than VIPC [$t(9) = 2.77$, $P < 0.05$] (see Fig. 5).

The same analysis was performed on the signal values obtained for the left DIPC in comparison to the right DIPC. None of the interactions of load and information type with area were significant (Ps > 0.1). Thus, the left DIPC was not functionally dissociable from the right DIPC.

Nonverbal working memory

Our results suggest that the DIPC is active when memory load is high regardless of information type. To provide further evidence for this claim, we performed voxelwise ANOVAs comparing the imaging data from the Korean high- and low-load conditions using

the criteria we established for the simple load and information-type contrasts (see Voxelwise tests). For both tasks and magnets, the left DIPC showed greater activity in the high-load nonverbal condition than in the low-load nonverbal condition (1.5-T N-back = −35, −50, 43/−23, −68, 36; 1.5-T item recognition = −27, −62, 45/−44, −40, 43/−32, −47, 35; 3-T N-back = −48, −44, 43; 3-T item recognition = −36, −46, 38/−26, −59, 34). In contrast, activity of the VIPC did not emerge when memory load was high in the nonverbal conditions.

General discussion

Previous attempts at locating the neural instantiation of the phonological short-term store have assessed the effects of memory load or the type of stimuli to be encoded on brain activity. A
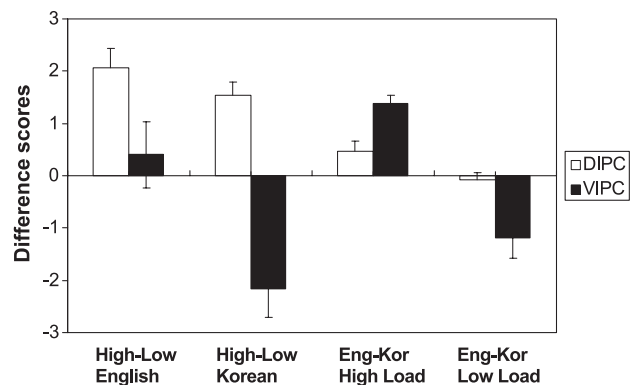

Fig. 5. Difference in mean signal values in simple load and information type contrasts for the VIPC and DIPC.

region that was more active when memory load was high or when linguistic stimuli were used was considered a potential candidate for such a store. Studies comparing verbal and nonverbal memory pointed to the VIPC as the site of the phonological STS, whereas others that manipulated memory load indicated involvement of the DIPC. In studies where load and information type were manipulated in the same set of subjects, direct comparisons of load but not information type were performed (D'Esposito et al., 1998; Reuter-Lorenz et al., 2000; Smith et al., 1996). Thus, confusion arose regarding the locus of the phonological STS, because load and information type were almost never manipulated or contrasted in the same design. It was unclear whether these anatomically nonoverlapping regions were functionally distinct or whether the peak of parietal activity varied widely across studies. By manipulating both these variables in the same design, we were able to demonstrate that these regions of the inferior parietal cortex behave quite differently in response to variations of load or the type of the items to be remembered. Moreover, the areas responded in ways that we predicted; the DIPC was more sensitive to load manipulations, whereas the VIPC showed a preference for the type of material to be remembered.

Based on our experiment, we can also explain why inferior parietal locations have varied across previous working memory studies. When low-load conditions are subtracted from high-load conditions, DIPC, but not VIPC, activity is manifested. This is in accordance with reports of DIPC activity in a wide variety of working memory tasks that implement a control condition that places little or no demand on working memory. Indeed, the only study to manipulate and directly contrast both load and information type in the same design found greater activity in the left DIPC in the object working memory condition than in the verbal working memory condition (Nystrom et al., 2000).

We also were able to demonstrate that VIPC activity is contingent upon the type of information to be remembered—a result consistent with earlier reports of VIPC activity in studies that used a nonverbal condition with a similar load as a control. Although DIPC activity tended to be higher for English letters in the high-load condition in the N-back task, the effect was reversed in the item-recognition task—a result that may explain why this area has not been found in item-recognition studies comparing verbal and nonverbal stimuli (Paulesu et al., 1993, 1996; Salmon et al., 1996). Martin et al. (in press) have reported similar results in their study of phonological and semantic verbal working memory. They took the parietal ROIs reported in Becker et al. (1999) and examined how they were affected by load and task type (i.e., semantic or phonological). They found that the DIPC was recruited more heavily when load was high regardless of the type of task being performed, whereas the VIPC was unaffected by memory demand. Instead, VIPC activity was affected by whether the task was phonological or semantic; activity of this region was greater when the task was phonological.

This experiment strongly supports our hypothesis that DIPC and VIPC are functionally dissociable. Our use of a complete experimental design allowed us to replicate prior observations of load effects in DIPC and information type in VIPC, but it also revealed unexpected complexities in the activation patterns. As discussed below, neither region behaves in a manner entirely consistent with current ideas of how verbal items are maintained in memory.

Dorsal inferior parietal cortex

Across magnets and tasks, the DIPC displayed robust load effects. However, we predicted that a region acting as a phonological short-term store should be more active in verbal than nonverbal memory conditions. The DIPC (1) did not show greater activity for verbal items, (2) was recruited more heavily in the nonverbal than the verbal high-load condition in the item-recognition task, (3) was not functionally dissociable from the right DIPC, and (4) displayed load effects in the nonverbal task. These results suggest that the DIPC may be acting as part of a frontal–parietal executive system (Corbetta et al., 2000; Posner and Dehaene, 1994). In our experiment, DIPC activity was modulated by load and information type similarly to two other regions, the left DLPFC and right DIPC, posited to be part of a general attentional network (Smith et al., 1996; Wojciulik and Kanwisher, 1999). Indeed, some researchers have speculated that the inferior parietal cortex serves to focus attention on items in working memory rather than serving as a phonological store per se (Chein et al., in press; Cowan, 1999). As part of a frontal–parietal executive system, it is not surprising that the DIPC is involved in working memory tasks employing a variety of verbal, spatial, and visual stimuli. This region may be important for retaining temporal order information (Marshuetz et al., 2000), attentionally reactivating sources of information in neural regions (Corbetta et al., 2002), rapid switching of attention (La Bar et al., 1999), or preparing for a given task (Sohn et al., 2000)—all domain-general functions that may be tapped in verbal working memory tasks.

Ventral inferior parietal cortex

On the surface, the VIPC would appear to be the most likely candidate for the phonological short-term store. Activation of this area has been reported in working memory tasks manipulating information type (Paulesu et al., 1993, 1996; Salmon et al., 1996) and in passive listening paradigms (Fiez et al., 1996; Petersen et al., 1998). Moreover, patients suffering from a selective short-term memory deficit have damage at or near this area (Shallice and Vallar, 1990; Vallar and Papagno, 1995). Accordingly, the VIPC was more active in the English high-load condition compared to the Korean high-load condition in three of the four information-type contrasts.

Despite fitting so many of the criteria of a short-term store, this region displayed two inconsistent findings. First, there was no difference between the verbal high- and low-load conditions. Although inconsistent with notions of a dedicated phonological store, this results in line with evidence of VIPC involvement in more basic speech processing such as phonological discrimination and identification tasks (Caplan et al., 1995), reading (Paulesu et al., 1996; Rumsey et al., 1997), the mediation between auditory and articulatory representations (Hickok and Poeppel, 2000), and auditory imagery (McGuire et al., 1996; Shergill et al., 2001). Thus, the VIPC may be more sensitive to the amount of phonological encoding or recoding that occurs in a given condition, rather than how much needs to be recalled.

The other result that conflicts with its potential role in phonological storage concerns the greater involvement of the VIPC in conditions where memory load was low or nonexistent (i.e., 0-back, detect, fixation). A study by Greicius et al. (2003) reported a similar result; that is, they found the VIPC to be more active in a spatial 0- than 2-back condition. It may be that activity in this area is inhibited by the central executive in cases where people are

purposefully trying to maintain items in working memory. In the verbal conditions, once the items are encoded and placed in short-term memory, it may be sensible for the store to block further input from more basic processing areas. A certain amount of noise may be introduced into the phonological buffer if phonological processors are allowed unrestricted input into the short-term store. If this were true, one would have to assume that the VIPC is suppressed regardless of the number of items being maintained. In the nonverbal high-load condition, activity of nonessential areas may also be occurring due to its general difficulty, and in fact, suppression of this area may be easier than in the verbal conditions, because there is no need to use the verbal system at all.

Although these explanations of VIPC activity need to be tested, the evidence is not supportive of its role as a phonological short-term store. This is puzzling given that some have suggested that this area is damaged in patients exhibiting a verbal working memory deficit without a concomitant impairment in phonological processing (Shallice and Vallar, 1990; Vallar and Papagno, 1995). Evidence for this claim, however, is based on the occurrence of common lesion sites reported across studies of short-term memory patients; thus, the types of tests used to assess spatial working memory and phonological processing deficits differ widely across these studies. Only one study has examined lesion sites within a large group of patients with verbal short-term memory deficits (Bartha and Benke, 2003). This study finds that the common area of damage for conduction aphasics with low verbal spans but normal auditory processing and spatial spans was in an inferior temporal region (BA 37). Although this region of the temporal lobe is not commonly reported in imaging studies of verbal working memory, it is possible that activity of a phonological store occurs so fleetingly that it goes undetected by current imaging techniques.

Rehearsal-related regions

While neither parietal region displayed the predicted interaction effect of load and information type, we also examined the activation in areas commonly associated with articulatory rehearsal in verbal working memory: Broca's area, the SMA, and bilateral cerebellar cortex. All these regions behaved in a way consistent with their presumed role in verbal working memory. Specifically, they were recruited most heavily in the verbal, high-load condition. One explanation for these results is that, as suggested by Baddeley and Hitch (1974), the rehearsal system refreshes verbal items in a short-term store, but that activity of the store is so transient that it is not detected by current imaging techniques. Alternatively, our findings may indicate that verbal working memory can be carried out solely by articulatory mechanisms (Gruber, 2001). Additional evidence for this claim is provided from a study by Chein and Fiez (2001) who reported sustained activation of Broca's area, but not parietal cortex, during the maintenance interval of a delayed serial recall task. Moreover, it has been suggested that Broca's area supports phonological storage as well as rehearsal. Sakai et al. (2002) asked participants to perform a distractor task during the memory delay of an item-recognition task. After the distractor interval, Broca's area and the parahippocampus were active at retrieval, but the parietal cortex was not, prompting Sakai et al. (2002) to suggest that Broca's area may serve to store information that is then reactivated by the parahippocampus. Thus, evidence is accumulating for the notion that items can be stored and maintained by traditional rehearsal areas without recourse to the parietal cortex.

Conclusions

Clearly, dorsal and ventral regions of the supramarginal gyrus respond in a distinct and dissociable manner during the performance of working memory tasks. Indeed, their performance was quite disparate across a number of conditions. Whereas the VIPC was responsive to the type of information to be maintained but not to memory load, the DIPC displayed the inverse pattern. Furthermore, VIPC activity was active in conditions with low memory demand, whereas the DIPC was more active when memory load was high.

We have proposed several ideas to explain the pattern of activity observed in these two parietal regions. The VIPC may be involved in more basic speech processes that are suppressed during working memory tasks. Rather than being selective for verbal material, the DIPC may contribute to executive processes such as retaining temporal order (Marshuetz et al., 2000), attentionally reactivating sources of information in neural regions (Corbetta et al., 2002), or task preparation (Sohn et al., 2000). However, neither area is affected by load and information type effects in a way predicted by a region serving as a phonological short-term store.

Acknowledgment

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