

Left parietal cortex is modulated by amount of recollected verbal information

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In two earlier experiments, we reported that left parietal cortex activity covaried with the amount of pictorial information recollected. The present experiment addressed the question whether our earlier results would generalize to verbal materials. Participants studied a series of word pairs and were then tested on individual old and new words in a modified remember/know task. In this task, participants were required to indicate whether recollection was accompanied by retrieval of study pairmates or not. As before, we operationally defined 'amount recollected' as the contrast between these two types of remember response. We found that the same left parietal region previously identified as sensitive to amount of recollected pictorial information is also sensitive to amount of recollected

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Introduction

Functional neuroimaging studies of recognition memory consistently report retrieval success effects (enhanced activity for correctly identified 'old' vs. 'new' test items) in left posterior parietal cortex, but the functional significance of these effects remains unclear. Three general classes of hypotheses have been advanced to explain retrieval success effects in left posterior parietal cortex [1]. The 'output buffer' hypothesis proposes that the region plays a role in the maintenance of retrieved information in a working memory store. The 'accumulator' hypothesis states that the region accumulates evidence in favor of a positive recognition decision [2]. Finally, the 'attentional reorienting' hypothesis proposes that the region acts to redirect attention from the external environment toward retrieved mnemonic content. Wagner *et al.* [1] also posited a second 'attentional' hypothesis according to which the left posterior parietal cortex supports the maintenance of attention toward recollected content. It is unclear, however, the degree to which this proposal differs from the output buffer hypothesis. As noted by Wagner *et al.* [1], these hypotheses need to be integrated with an extensive body of evidence [3] indicating that recognition is supported by two independent processes: recollection and familiarity. Although recognition associated with recollection – the retrieval of qualitative information (e.g. contextual details) about a study episode – is associated with retrieval success effects in both superior and inferior regions of the left posterior parietal cortex, recognition based on familiarity – an acontextual sense of prior occurrence – is associated solely with retrieval

success effects in left superior posterior parietal cortex (for review, see Ref. [4]).

In two earlier experiments, we attempted to adjudicate between the output buffer and attentional reorienting hypotheses as they apply to recollection-related activity in left inferior posterior parietal cortex [5,6]. We argued that recollection-related activity in a region supporting the reorienting of attention toward the contents of retrieval should vary solely according to whether or not recollection occurs, because attentional reorienting is usually conceived of as an all-or-none phenomenon. In contrast, activity in a region supporting the maintenance of recollected content should vary according to the amount of information that needs to be maintained – analogous to 'load' effects in regions held to support the maintenance of information in working memory [7]. In the first of these experiments [5] – the one most relevant here – participants studied pairs of object images, and then underwent a memory test in which individual objects were used as test items in a modified remember/know procedure. Participants were instructed to make one response (R2) if they could recollect the test item and its studied pairmate, another response (R1) if they could recollect some information from the study episode but not the pairmate, a third response (K) if the test item was judged to have been studied in the absence of any recollection of study details, or a fourth, New, response. We assumed that trials on which old items received R2 responses were on average associated with recollection of more study information than when old items were given R1 responses, and this assumption was

validated by post-test results [5]. Thus, we operationally defined 'amount recollected' as the contrast between these two trial types (i.e. R2 hits > R1 hits). This contrast revealed a region on the border of left inferior lateral posterior parietal and occipital cortex (BA 39/19) where activity varied according to amount of information recollected. We argued [5,6] that this finding is consistent with the proposal that this region plays a role in the maintenance of recollected content, rather than acting to reorient attention to retrieved content.

In our earlier studies [5,6], the experimental materials were exclusively pictorial. The question remains, therefore, whether the findings generalize to other classes of recollected content. If, as we have argued [4–6], left inferior posterior parietal cortex supports the representation of recollected content in an amodal manner (*c.f.* [8]), then left inferior parietal activity should also be modulated by amount of recollected information when nonpictorial materials are employed. Accordingly, this study addressed the question of whether left inferior posterior parietal cortex is sensitive to amount of information recollected for verbal rather than pictorial information.

Methods

In each of the three study blocks, participants generated sentences from 40 visually presented word pairs sampled from a pool of 522 nouns (length of 3–9 letters, Kucera–Francis written frequency between 0 and 86, maximum horizontal visual angle of 6.4°) obtained from the MRC Psycholinguistic Database (http://www.psy.uwa.edu.au/mrcdatabase/uwa_mrc.htm). Participants were instructed to speak the sentence generated for each word pair aloud and press any key to continue to the next trial. On each study trial, one word was presented to the left of fixation and another word was presented to the right. The location of each stimulus in a pair was assigned randomly. Each study block was immediately followed by a scanned test phase. At test, individual words were presented centrally and old words were always taken from the left half of the study display. Stimuli were presented in an upper case white font against a black background on a screen positioned at the back of the scanner bore visible through a mirror attached to the head coil.

At test, participants performed the same modified remember/know task that was employed by Vilberg and Rugg [5] (described above). Twenty-three participants (12 females; age range = 18–29 years; mean age = 21; all of whom gave informed consent before participation, in accordance with the UCI Institutional Review Board, which approved the study) undertook the three study-test cycles after receiving task instructions and completing a short practice session. After completion of the first practice test, participants were asked to report

the identity of words given R2 responses to verify their understanding of task instructions. Five participants were excluded from all analyses because of insufficient responses (fewer than 10 trials) in one or more critical response categories.

Functional MRI data were acquired during the three test sessions, each consisted of 60 item trials, 20 fixation-only trials, and three buffer trials placed at the beginning of each test block. Each test trial consisted of the presentation of a red fixation cross for 500 ms, a test item (40 old, 20 new) for 500 ms, and then a black fixation cross for 2500 ms. Participants responded through a button box as in Vilberg and Rugg [5] (see also for details of trial counterbalancing and randomization). Immediately after completing the third test block, a surprise post-test was administered. Each item from the last test block endorsed as R2 or R1 was displayed individually and participants were required to report the identity of each item's pairmate, responding 'pass' if it could not be recollected. Structural MRI data were acquired after completion of this post-test.

MRI data were acquired using a 3T Philips Achieva MRI scanner (Philips Medical Systems, Andover, Massachusetts, USA). Data acquisition parameters (for both functional and anatomical scans) were identical to those described by Vilberg and Rugg [9] except that, here, 160 volumes were acquired during each test session, and functional data were spatially realigned through a two-step process wherein all volumes were aligned to the first image of the time series and subsequently aligned to the mean across-volume image. Data were modeled as described in Vilberg and Rugg [5], with the exception that Misses (studied items misclassified as new) were defined as events of no interest due to lack of sufficient trials for most participants. Thus, the model included R2 hits, R1 hits, K hits, correct rejections (CRs), and events of no interest. A cluster extent-threshold of 5 voxels was employed for all contrasts. Unless otherwise noted, unidirectional contrasts were height-thresholded at *P* value of less than 0.001, whereas inclusive and exclusive masks were thresholded at *P* values of less than 0.01 and 0.05, respectively. Small volume corrections (SVC; [10]) were employed to determine the reliability (*P* < 0.05) of regional effects that were predicted *a priori*. All coordinates are reported in MNI space. For the purpose of visualization of the findings, Caret software [11] was used to map cortical regions of interest onto inflated fiducial brains through average fiducial mapping onto the PALS-B12 atlas [12,13] in SPM5 space.

Results

The mean hit rate was 86%, against a correct rejection rate of 92%. The proportions of old and new items attracting each class of response, and the associated response times,

are given in Table 1. As seen from the table, participants rarely false alarmed, and distributed their old judgments in favor of R2 responses. A repeated-measures analysis of variance on mean test response times (RTs) (K hits, R1 hits, R2 hits, and CRs) revealed a significant main effect of response type [$F(2.4, 40.6) = 55.20, P < 0.0001$]. Pairwise comparisons of test RTs using t -tests revealed that RTs to CRs were shorter than those to each type of hit (all $P < 0.001$). In addition, R2 RTs were shorter than both K and R1 hit RTs (both $P < 0.001$). R1 and K hit RTs did not significantly differ ($P > 0.1$).

The mean correct recall rates for the pairmates of items given R2 and R1 responses during the final test block were 82% (SD = 17%) and 31% (SD = 5%), respectively; these rates differed significantly [$t(17) = 9.32, P < 0.001$]. On the basis of this finding, we assume that R2 trials were on average associated with the retrieval of quantitatively more information than R1 trials, justifying the use of the R2 > R1 contrast to identify regions sensitive to amount recollected (see below).

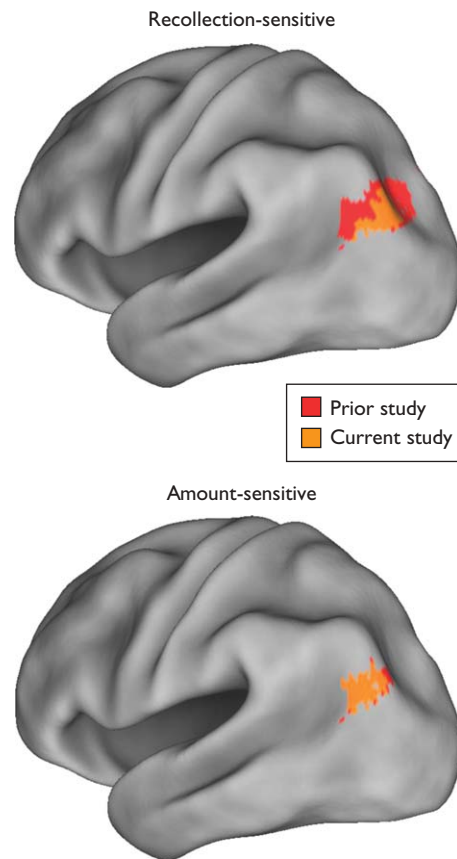
First, we used SVC to test our prediction regarding the overlap of recollection-sensitive left parietal activity in our earlier and current studies. To do this, we created a mask that defined the recollection-sensitive left parietal cluster from our earlier study [5], and then performed an SVC within this cluster on the analogous recollection-sensitive contrast in the present experiment. The mask was created by the contrast of R2 + R1 hits > K hits thresholded at P value of less than 0.001, exclusively masked by K hits > misses at P value of less than 0.05 [5]. Recollection-sensitivity in this study was identified by the contrast of R2 + R1 hits > K hits at P value of less than 0.01, exclusively masked by K hits > CRs at P value of less than 0.05. After SVC, this contrast revealed a 40-voxel cluster within the masked region (peak x, y, z coordinates $-36, -84, -30, z$ -score = 3.69, corrected $P < 0.005$). Figure 1 (top) displays the overlap between the left inferior posterior parietal regions identified as recollection-sensitive in this and our previous study. An additional analysis using a subset ($n = 12$) of participants who contributed 10 or more mistrials (where previously studied items were incorrectly identified as new) verified

Table 1 Proportions and RTs of old and new items attracting each response type

Response	Proportions		RTs	
	Old	New	Old	New
R2	0.37	0.01	1614 (231)	–
R1	0.28	0.00	1864 (310)	–
K	0.21	0.01	1917 (327)	–
New	0.12	0.92	1848 (325)	1296 (206)

Response proportion columns do not sum to 1.00 because of exclusion of response omissions. RTs are displayed in ms, with standard deviations in parentheses. Too few participants contributed sufficient false alarms to permit meaningful evaluation of their RTs.

Fig. 1

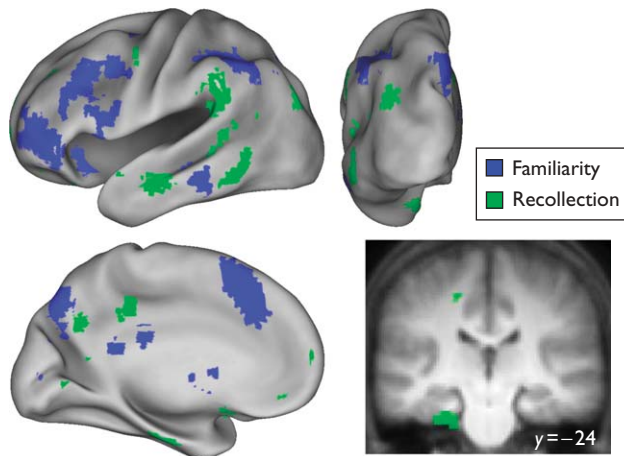


Top: orange demarcates the overlap of recollection-sensitive voxels from this study within the cluster identified as recollection sensitive in our earlier study [5]. Recollection-sensitive left posterior parietal voxels from our earlier study that were not also recollection sensitive in this study are shown in red. Bottom: amount-sensitive voxels of this study which fall within the previously identified amount-sensitive left posterior parietal cluster [5] are displayed in orange. Amount-sensitive left posterior parietal voxels from the earlier study which were not also amount-sensitive in this study are shown in red. Effects are mapped onto inflated fiducial brains.

that the use of CRs in place of misses in the current contrast did not affect the findings. In this analysis, we used the same contrast as that used by Vilberg and Rugg [5] to identify recollection-sensitive regions and applied the SVC to the masked region. The analysis revealed a recollection-sensitive cluster within the masked region which survived SVC (corrected $P < 0.05$).

Next, we addressed the question whether lateral parietal regions sensitive to amount of information recollected also overlapped between this and earlier studies. To do this, we first created a mask of the left parietal amount-sensitive effect in the earlier study (R2 > R1 hits at $P < 0.01$ inclusively masked by R2 + R1 hits > K at $P < 0.001$ and exclusively masked by K hits > misses at $P < 0.05$; [5]). We then identified amount-sensitive effects in the current experiment with the R2 > R1 hit

Fig. 2



Left hemisphere cortical regions selectively sensitive to recollection (green) and familiarity (blue) as identified by whole brain voxel-wise analysis (results thresholded at $P < 0.005$ for display purposes). The recollection-sensitive left medial temporal cluster is displayed on a section ($y = -24$) of the across-participant mean anatomical image.

contrast ($P < 0.01$), and applied an SVC to this contrast using the aforementioned amount-sensitive mask. This analysis revealed a 33-voxel cluster (peak x, y, z coordinates $-48, -72, 27$, z -score = 3.51, corrected $P < 0.01$). Figure 1 (bottom) displays the overlap between the amount-sensitive left parietal regions identified in the two studies.

Finally, we performed exploratory whole brain analyses to identify regions specifically sensitive to recollection versus familiarity. Recollection-sensitive regions were identified by exclusively masking the $R2 + R1$ hits $>$ K hits contrast with the K hits $>$ CRs contrast. Familiarity-sensitive regions were identified by exclusively masking the K hits $>$ CRs contrast with the $R2 + R1$ hits $>$ K hits contrast. Regions showing familiarity-related increases in activity included left lateral, anterior, and medial prefrontal cortex, bilateral caudate, left intraparietal sulcus, and precuneus. Regions showing recollection-related increases included left inferior, middle, and superior temporal gyri, as well as the superior frontal gyrus, left inferior posterior parietal cortex, precuneus, and left entorhinal cortex. Figure 2 illustrates the regions identified as recollection-sensitive versus familiarity-sensitive by these whole brain analyses (peak maxima of clusters identified in these analyses are available from the authors by request).

Discussion

The present findings replicate and extend the findings of our earlier study that used pictorial stimuli [5]. Specifically, recollection-sensitive and amount-sensitive clusters were identified in the left inferior parietal/

occipital cortex, and these clusters overlapped with the analogous effects identified in our earlier experiment. Thus, our earlier findings generalize to nonpictorial stimulus materials, suggesting that these recollection-related effects are not correlates of material-specific or modality-specific processes (for example processes supporting visual imagery). The findings therefore provide support for the proposal that left inferior posterior parietal cortex in the vicinity of the angular gyrus plays a generic role in the maintenance or representation of recollected information [5]. As with our earlier results, the present findings seem to be inconsistent with the alternative proposal that this region supports attentional reorienting to recollected content [14–16].

The present and earlier findings also pose difficulties for the ‘accumulator’ hypothesis of the role of left posterior parietal cortex activity in recognition memory, at least as articulated by Wagner *et al.* [1] (see also Ref. [2]). By this hypothesis, left lateral parietal activity tracks the amount of evidence supporting a positive recognition decision. Present and earlier findings that left inferior parietal activity does not differ between test items accorded ‘New’ and ‘K’ judgments are difficult to reconcile with this hypothesis. Notably, a pairwise contrast on the parameter estimates for K hits and CRs extracted from the peak of the present amount-sensitive left parietal effect was nonsignificant ($t < 1$). Of course, this does not mean that other regions (in left superior lateral posterior parietal cortex or elsewhere) may not show the more continuous gradations in retrieval-related activity that would be expected of a region supporting accumulation of generic evidence about the study status of a test item (for e.g., see Refs [6,17]).

As in earlier studies [5,6,18,19], whole brain analyses revealed brain regions that were selectively sensitive to familiarity versus recollection, with a superior–inferior division emerging within left lateral posterior parietal cortex according to whether recognition was familiarity-driven or recollection-driven. These findings are consistent with previous reports that the neural correlates of recollection and familiarity are dissociable (see citations above).

Conclusion

The present data support earlier claims that left inferior parietal/occipital cortex participates in the online representation of recollected content. The data further suggest that the recollection-related processes supported by this region are not restricted to visual object information.

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