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Dissociation of the neural correlates of recognition memory according to familiarity, recollection, and amount of recollected information

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Abstract

The present experiment used fMRI to investigate whether neural correlates of recognition memory behave in a manner consistent with the proposal that recognition decisions are based on a unidimensional memory strength variable. A modified remember/know recognition test was used in which participants could indicate two levels of recollection. Participants were required to indicate whether a test item was new, familiar (known), elicited recollection of general contextual details from the study episode (R1 response), or elicited a specific recollection of the item with which it was paired at study (R2 response). Little evidence could be found to support the view that Remember/Know/New judgments reflect variations along a single strength dimension. Instead, the findings replicated prior research in indicating that the neural correlates of recollection and familiarity can be doubly dissociated. Two recollection-sensitive regions - left lateral inferior parietal and left fusiform cortex - were found to be sensitive to amount of information recollected, as operationalized in the contrast between R2 and R1 responses. It is proposed that these regions may support the representation of recollected information.

Keywords

memory strength; fMRI; parietal; hippocampus; dual-process; brain imaging

Dual-process models of recognition memory propose that recognition is based on the outcome of two independent processes, recollection and familiarity. The former process involves the retrieval of specific details of a past experience whereas the latter depends on an acontextual sense that an event has been previously experienced. Several event-related fMRI studies have attempted to dissociate the neural correlates of these two processes. Among the brain regions identified in these studies, the left inferior lateral parietal cortex (Brodmann Area (BA) 39/40) has been consistently linked to recollection (Henson et al., 1999; Henson et al., 2005; Woodruff et al., 2005; Wheeler and Buckner, 2004; Shannon and Buckner, 2004; Vincent et al., 2006). More superior parietal regions (BA 7/40) have been associated not with recollection, but with positive recognition judgments more generally (Wheeler and Buckner, 2003). In a recent study, superior parietal cortex displayed activity that was graded according to level of reported familiarity but insensitive to recollection (Yonelinas et al., 2005). In the same study, a more

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inferior left parietal region displayed greater activity for recollected than highly familiar items, but did not differentiate levels of familiarity. Together, these findings suggest that recognition-sensitive activity in lateral parietal cortex can be dissociated according to whether or not recognition is accompanied by recollection.

An important focus of the present study concerns the functional significance of recollection-related lateral parietal activity. In a recent event-related potential (ERP) study, the amplitude of the 'left parietal old/new ERP effect' (an electrophysiological correlate of recollection; Rugg et al., 2002) was found to vary according to amount of information recollected (Vilberg et al., 2006; see also Wilding, 2000). On the assumption that the ERP effect reflects recollection-sensitive activity in lateral parietal cortex, lateral parietal activity should be sensitive to the amount of information recollected when assessed directly with fMRI. The present study provides the opportunity to test this prediction.

Thus, the present study addressed the question whether there are recollection-sensitive regions where activity is modulated by amount of information recollected. We employed the modified Remember/Know test procedure adopted in our prior ERP study. Briefly, subjects are presented with picture pairs at study. At test, only single items are presented. The requirement is to signal not merely whether a recognized item was recollected or familiar (the standard Remember/Know distinction), but whether recollection included retrieval of the item's studied pairmate (Remember 2 response), or was limited to other contextual details only (Remember 1 response). For the reasons detailed in the Discussion, we assume that, in general, Remember 2 responses were associated with recollection of more information than Remember 1 responses were. As already noted, we predicted that left inferior lateral parietal cortex would be sensitive to amount of recollected information. Additionally, the study sought to further assess the extent to which the neural correlates of recollection and familiarity can be fractionated. In particular, we took advantage of our experimental procedure to contrast the predictions derived from dual- vs. single-process models of recognition. Unlike the former class of models, single-process models assume that familiarity and recollection reflect differences in the strength of a common memory signal (e.g., Gillund and Shiffrin, 1984; Donaldson, 1996; Dunn, 2004; see Gonsalves et al., 2005 for relevant neuroimaging findings). That is, these models assume that recollection and familiarity differ in a quantitative rather than a qualitative sense. If this is the case, then it should be possible to identify regions where activity varies as a function of the 'strength' of the memory signal elicited by a test item. Accordingly, we attempted to identify regions where recognition-related activity varied in a linear fashion according to the 'strength' of the memory elicited by a test item, on the assumption that items endorsed as new were associated with the lowest strength, those given a Know response with intermediate strength, and those endorsed as Remembered elicited the strongest signals (Gonsalves et al., 2005).

Materials and Methods

The data reported below were obtained in two independent experiments, employing non-overlapping subject samples. With a few minor exceptions (as noted) the experimental procedures were identical. Hence the experiments are described together.

Subjects

Twenty-three [7 females; 18 - 27; mean age = 21.3 (SD = 2.3)] and twenty-two [12 females; 18 - 22; mean age = 19.9 (SD = 1.3)] native English speakers took part in Experiments 1 and 2, respectively. Subjects reported themselves to be free of neurological disease and other contraindicated conditions for participation in an fMRI experiment. All but one subject reported right-hand dominance. In accordance with the requirements of the UCI Institutional Review Board, which approved the research program, all subjects gave informed consent prior to participating. For Experiment 1, nine subjects' data were excluded due to insufficient trials

(fewer than 10) in one or more of the critical response categories (K hits, R1 hits, R2 hits, correct rejections, and misses). For Experiment 2, eight subjects' data were excluded due to insufficient trials in one or more of the critical response categories. Thus, data from 14 subjects in each experiment are reported below.

Experimental materials and procedure

Each experiment consisted of one study and one test session. Scanning occurred during the test session only, although both sessions were undertaken inside the scanner. VisuaStim XGA MRI compatible goggles (Northridge, CA, USA; FOV = 640×480 pixels, 30° visual angle) were used to present stimuli during both sessions. Study and test stimuli were color pictures of objects on grey backgrounds selected from a pool of 403 pictures of objects previously used by Smith et al. (2004). For each subject in Experiment 1, 240 pictures were randomly selected to serve as study stimuli, 60 to serve as new test stimuli, and an additional 30 to serve as buffer and practice stimuli. For each subject in Experiment 2, 288 pictures were selected randomly to serve as study stimuli, 72 as new test stimuli, and 30 as buffer and practice items.

Prior to performing the study phase, subjects performed practice versions of the study and test tasks (12 and 18 trials, respectively) outside the scanner. Just prior to undertaking each task, both verbal and written instructions were administered. The instructions were later repeated verbally just prior to each phase of the experiment proper. To ensure compliance with the instructions regarding 'Remember 2' responses (see below), immediately following the practice test session subjects were required, for each test item endorsed as Remember 2, to name the object with which it had been paired at study.

At study, subjects viewed pairs of color pictures on a grey background (120 pairs and 144 pairs in Experiments 1 and 2, respectively). The two pictures occupied different corners of the display frame, and the locations employed varied randomly across trials (examples of study and test displays are shown in Figure 1). The task requirement was to imagine how the objects depicted in the pictures might interact. In Experiment 1, the display of the objects was terminated by a button press signaling when a good visual image had been formed or after 8 s had elapsed. In Experiment 2, the presentation duration was fixed at 3 s. In both experiments, the study trials were presented sequentially with no appreciable inter-trial interval. A short rest break occurred after half of the study trials were completed.

At test, all stimuli were presented at fixation. Subjects viewed single pictures (120 old and 60 new, and 144 old and 72 new, in Experiments 1 and 2 respectively). The task requirement was based on the Remember-Know procedure. Unlike the standard procedure, however, in the version of the task employed here subjects were able to indicate the amount of information they recollected in response to each test cue. Four responses were possible: A 'Remember 2' (R2) response was to be used when the item paired with the test picture could be recollected; a 'Remember 1' (R1) response was required when the test item elicited recollection of details of the study episode but not the associated picture; a 'Know' (K) response was required when the test picture was judged to be old, and no details could be recollected about encoding episode; a 'New' response was to be used when the test picture was judged new, or when its study status was unknown.

Each test trial consisted of the presentation of a red fixation cross for 500 ms, followed by the test picture for 500 ms, followed by a black fixation cross which remained on the screen for 2000 ms. Old and new stimuli were randomly interspersed with null events (60 and 72 for Experiments 1 and 2, respectively for each subject). During these null events, a black fixation cross remained on the screen for the entire trial duration. A one-minute break was given half-way through the test trials. For half of the subjects the index finger of the left hand was used to indicate New judgments, and the index, middle, and ring fingers of the right hand were used

to indicate K, R1, and R2 responses respectively. This hand assignment was reversed for the remaining subjects.

Approximately 20 minutes after completion of the test session, post-tests were administered outside the scanner. In the first post-test, administered in both experiments, subjects were shown individual test pictures to which they had previously responded R2 and were asked to name the pictures' pairmates. The second post-test was administered to subjects in Experiment 2 only. The subjects were shown each test picture to which they had responded R1 and were asked to report their reason for giving the response. Additionally, subjects were asked to report whether they could recollect the item with which the test picture had been paired, and if so, to indicate whether this information had been available during the test session in the scanner.

MRI data acquisition

High-resolution T1-weighted anatomical images (256×256 matrix, 1 mm^3 voxels) and blood oxygenation level-dependent (BOLD), T2*-weighted echoplanar functional images (64×92 matrix, FOV = 25 cm, TR = 2500 ms, TE = 40 ms) were acquired using a 1.5T Philips Eclipse MRI scanner (Philips Medical Systems, Andover, MA). Three-hundred and twenty six volumes (experiment 1) and three-hundred and eighty six volumes (experiment 2) were acquired. Each volume comprised 27 slices oriented parallel to the AC-PC line ($2.6 \text{ mm} \times 3.9 \text{ mm}$ pixels, thickness 3mm, 1.5mm inter-slice gap) acquired in a descending sequence. The first 5 volumes of the session were discarded to allow equilibration of tissue magnetization.

Data analysis

Statistical Parametric Mapping (SPM2, Wellcome Department of Cognitive Neurology, London, UK), run under Matlab 6.5.1 (The Mathworks Inc., USA) was used for fMRI data analysis. Functional images were subjected to slice timing correction (using the middle slice as the reference), realignment (to the first volume), reorientation, spatial normalization to a standard EPI template (based on the Montreal Neurological Institute (MNI) reference brain; Cocosco et al., 1997) and smoothing using an 8mm FWHM Gaussian kernel. Analysis was performed using a General Linear Model (GLM) in which a delta function was used to model neural activity at stimulus onset. This function was convolved with the canonical haemodynamic response function (HRF) and its temporal and dispersion derivatives to model the BOLD response (Friston et al., 1998). The analyses of the parameter estimates of the temporal and dispersion derivatives added little to the findings obtained with the canonical HRF, and therefore are not reported.¹ Six event-types (R2 hits, R1 hits, K hits, Correct Rejections (CR), Misses (M), along with events of no interest such as buffer trials, and trials with incorrect or omitted responses) were modeled. The model also included as covariates the across-scan mean and six regressors representing motion-related variance (three for rigid-body translation and three for rotation). An AR(1) model was used to estimate and correct for nonsphericity of the error covariance (Friston et al., 2002). The GLM was used to obtain parameter estimates representing the activity elicited by the events of interest.

In a preliminary analysis, random-effects contrasts were conducted on parameter estimates derived from a model in which experiment was included as a between-subjects factor. In this analysis, the principal contrasts of interest ($K > M$, $R1 + R2 > K$, and $R2 > R1$) interacted with the factor of experiment in only a single case in one small cluster.² Accordingly, in the analyses

¹The principal contrasts of interest ($K > M$, $R > K$ and $R2 > R1$) were used to evaluate effects on activity modeled by the temporal and dispersion derivatives. Statistical thresholds were identical to those used for the canonical HRF (see text). With the dispersion derivative, significant effects were found in the cerebellum for the $R > K$ contrast (cluster size = 33 voxels, $Z = 4.61$, $p < 0.001$, MNI coordinates = $-18, -45, -15$). For the temporal derivative, effects were found for the $K > M$ contrast in the precuneus (cluster size = 27, $Z = 4.01$, $p < 0.001$, coordinates = $-15, -48, 48$) and posterior cingulate (cluster size = 9, $Z = 3.62$, $p < 0.001$, coordinates = $12, -33, 48$). Neither of these clusters overlapped with regions identified when modeling activity with the canonical HRF (see Results).

presented below, the data from the two experiments were collapsed. Unless otherwise noted, unmasked contrasts were thresholded at $p < 0.001$, uncorrected, with a 9 voxel extent threshold. When orthogonal contrasts were inclusively masked, their individual thresholds were set so as to maintain a conjoint significance level of $p < 0.001$ (as estimated with Fisher's procedure; Lazar et al., 2002). Nonorthogonal contrasts were inclusively masked with individual thresholds maintained at $p < 0.001$. Contrasts employed as exclusive masks were thresholded at $p < 0.05$ (note that the more liberal the threshold of an exclusive mask, the more conservative is the masking procedure). For the purpose of visualization of the findings, Caret software (Van Essen et al., 2001) was used to map cortical regions of interest onto inflated fiducial brains using the PALS-B12 atlas (Van Essen, 2002; Van Essen, 2005). A normalized mean anatomical image of the subjects included in the reported analyses was also created for the purposes of visualization.

Results

Behavioral Performance

Study—For Experiment 1, response times (RTs) at study were sorted according to subsequent response at test so as to permit a comparison with the findings of our prior ERP study that employed the same study procedure (Vilberg, Moosavi, and Rugg, 2006). Mean study RTs for pairs whose test items were later correctly identified as old with R2, R1, and K responses, and RTs for items incorrectly judged New (Misses) were 6340 ms, 6516 ms, 6481 ms, and 6069 ms, respectively. A repeated-measures ANOVA revealed a significant effect of response category, $F(1.5, 20.1) = 7.04, p < 0.01$. To determine whether the study RT results were similar to those in our prior ERP experiment, study RTs for pairs later associated with R2 and R1 responses were contrasted under the *a priori* prediction that the former would be faster. This prediction was confirmed (one-tailed $t(1, 13) = 3.06, p < 0.005$).

Test—For Experiments 1 and 2, the mean hit rates were 78% and 71%, against average correct rejection rates of 90% and 91%, respectively. The proportions of old and new items attracting each response type are given in Table 1, excluding response omissions. A repeated-measures ANOVA on the proportions of old items given K, R1, and R2 responses for the two experiments failed to reveal any significant effects of response type or experiment, all $p > 0.1$. The proportions of new items correctly identified as new for each group of participants were subjected to a two sample t-test. This analysis similarly failed to reveal an effect of experiment, $p > 0.9$.

Mean test RTs to old items are shown in Table 2 segregated according to response category (R2, R1, K, and Miss), along with the RTs to correctly rejected new items for each experiment. A repeated-measures ANOVA on the RTs for R2, R1, and K hits, Misses, and CRs revealed a significant main effect of response type, $F(3.0, 78.0) = 46.11, p < 0.0001$, but no effects involving experiment (all $p > 0.2$). Pairwise comparisons of test RTs using planned t-tests collapsed across the two experiments revealed that RTs to correct rejections and misses were shorter than those to each class of hit (K, R1, and R2) (all $p < 0.0001$). Unlike the results of our prior EEG experiment, RTs for R2 and R1 hits did not differ ($p > 0.2$).

Post-Test Recall—Recall of the study partners of items given R2 responses at test was evaluated in a post-test session for both Experiments 1 and 2. For the included subjects, the mean recall rates were 74% (SD = 23%) and 73% (SD = 23%) in experiments 1 and 2, respectively (note that these figures likely underestimate the true recall rate, as they are based

²The K > M contrast revealed a significant effect of experiment in the left middle temporal gyrus (cluster size = 10 voxels, $Z = 3.64, p < 0.001$, coordinates = $-45, -60, 0$).

on responses obtained outside the scanner some 20 min after the end of the original test session). For Experiment 2, subjects reported that they subsequently recalled the pairmate of an item endorsed as R1 on a mean of 10% (SD = 8%) of trials.

fMRI findings

We searched for memory strength effects by targeting regions that demonstrated monotonic increases or decreases in activity for old items accorded New (Miss), K, R1, and R2 responses respectively. Next, we identified regions that were selectively sensitive to either familiarity or recollection. Lastly, we determined which, if any, of these recollection-sensitive regions were also sensitive to amount of information recollected. To identify recollection-sensitive regions, a single category of remember (R) items was created by collapsing old items accorded R1 and R2 judgments. This provided a means of identifying recollection-sensitive effects that was unbiased with respect to the nature of the recollected content, and is equivalent to the undifferentiated 'Remember' judgments employed in prior studies (Eldridge et al., 2000; Henson et al., 1999; Woodruff et al., 2005). Misses were used as a 'baseline' condition so as to hold study history of items constant across contrasts. Results for the key contrasts were qualitatively very similar when correct rejections were employed instead of misses.

Memory strength—We were unable to detect any regions where recognition-related activity was graded according to memory strength - as operationalized by inclusive masking of the $R2 > R1$, $R1 > K$, and $K > M$ contrasts to search for monotonic increases in activity, and of the $M > K$, $K > R1$, and $R1 > R2$ contrasts to search for regions where activity decreased with increasing strength. This remained the case when the thresholds for the contrasts were reduced to $p < 0.05$; even at this liberal threshold, no clusters were revealed that contained more than three contiguously activated voxels.

The above analyses operationalized memory strength on the assumption that R2 responses were associated with greater strength than R1 judgments. To maximize the comparability of the findings with those of Gonsalves et al. (2005), who employed a standard Remember/Know task, we performed further analyses in which R1 and R2 response categories were collapsed, and correct rejections were included. These analyses searched for regions where activity differed ($p < 0.05$) according to 'strength' (inclusive masking of $CR < M$, $M < K$, $K < R$, and vice versa). These additional analyses revealed one cluster (9 voxels in extent) in the left superior frontal gyrus (peak voxel at $-3, 6, 57$) where activity increased with increasing strength, and no voxels demonstrating the reverse relationship.

Recollection vs. Familiarity—This set of analyses addressed the issue of the dissociability of the neural correlates of familiarity and recollection. Regions showing effects of familiarity that did not also show recollection effects were identified by exclusively masking the $K > Miss$ contrast with the $R > K$ contrast. The resulting regions included clusters in bilateral caudate nucleus, medial occipital/parietal cortex, left superior parietal cortex (BA 40/7), and left dorsolateral/anterior prefrontal cortex. Regions showing selective recollection effects were identified by exclusively masking the $R > K$ contrast with the $K > Miss$ contrast. The identified regions included left parietal/occipital cortex (BA 39/19), left anterior medial temporal cortex, and left prefrontal cortex superior to the prefrontal regions demonstrating a familiarity effect. Both sets of regions, that is, those specifically sensitive to familiarity and those specifically sensitive to recollection, are illustrated in Figure 2. Table 3 lists the peak maxima of the clusters identified by these analyses.

Unlike in several previous studies that contrasted recollection- and familiarity-related activity (Eldridge et al., 2000; Cansino et al., 2002; Wheeler and Buckner, 2004; Woodruff et al., 2005; Yonelinas et al., 2005), we failed to identify recollection-related activity in the

hippocampus when the contrast was based on activity elicited by items endorsed as recollected (R judgments), although such activity was identified in a left anterior medial temporal region possibly corresponding to the amygdala (Figure 2 and Table 3). When the contrast with K judgments was restricted to recollected items endorsed as R2, however, recollection-related activity was identified in a parahippocampal region just medial to the hippocampus (coordinates = $-18, -30, -18$; $Z = 3.18$). Relaxing the statistical threshold to $p < 0.01$ revealed that this activity extended along the medial temporal lobe, with an anterior peak in the hippocampus (coordinates = $-21, -21, -18$; $Z = 2.44$; see Figure 3). This anterior effect survived small volume correction for False Discovery Rate (Genovese et al., 2002) within a 5mm radius sphere centered on the peak of the left hippocampal recollection effect reported by Yonelinas et al. (2005). Similar, though statistically weaker, trends were evident for the $R1 > K$ contrast at the same loci (parahippocampal, $Z = 2.03$, $p < 0.025$; hippocampal, $Z = 1.78$, $p < 0.04$).

Amount of information recollected—Recollection-sensitive regions that were also sensitive to the amount of information recollected were identified by inclusively masking the $R > K$ and $R2 > R1$ contrasts, and then exclusively masking the result with the $K > M$ contrast to eliminate voxels also sensitive to familiarity. Clusters were identified in the right precentral gyrus, left fusiform gyrus and left inferior lateral parietal cortex (BA 39/19) (see Table 4). Figure 4 shows the left hemisphere effects along with the recollection-sensitive regions described previously.

Although we assume that R2 responses were accompanied by the recollection of more information than R1 responses, it is possible that the two types of R responses differ primarily on the basis of the content, rather than amount, of recollected information (e.g., picture-context associations in the case of R1 responses vs. picture-picture associations for R2 judgments). If this were the case, one would expect the $R1 > R2$ contrast to be as likely to identify regions differentiating the two classes of judgment as the reverse contrast. Accordingly, we performed an analysis exactly analogous to that employed to identify regions where recollection-related activity was enhanced for R2 judgments, but in this case searching for regions where R1 activity exceeded R2 activity. No voxels were identified by this analysis.

Discussion

The present findings combine with prior functional neuroimaging and ERP evidence to suggest that the neural correlates of recollection and familiarity are functionally and neuroanatomically dissociable (e.g., Yonelinas et al., 2005; Woodruff et al., 2006; Curran et al., 2006). The findings further permit a distinction to be drawn between recollection-sensitive regions on the basis of their sensitivity to amount of information recollected. Below, we expand on these points, and their implications for an understanding of the functional significance of the neural correlates of recollection.

Before turning to the fMRI findings, however, we comment on two salient features of the behavioral data. First, the pattern of response times obtained in the study session of experiment 1 indicated that trials containing items later endorsed as R2 attracted faster response times than those later endorsed as R1. This result, which replicates the findings of Vilberg, Moosavi, and Rugg (2006), lends credence to the assumption that the two categories of ‘remember’ response were associated with retrieval of different kinds of information: had subjects been selecting between these response options on the basis of non-mnemonic information, no relationship with study behavior would have been evident. The assumption is further supported by the performance of subjects when asked to recall the pairmates of items endorsed as R2 (experiments 1 and 2) or R1 (experiment 2 only). Even though the recall test was administered

outside of the scanner some 20 minutes after the fMRI session, recall was markedly more accurate for items associated with R2 than R1 judgments.

According to single-process models, recognition memory performance is based on the assessment of a single variable of memory strength. It is proposed that the functional properties of this memory signal do not differ according to whether a recognition judgment is associated with a 'Know' or a 'Remember' judgment (or, presumably, an R2 judgment). Rather, these judgments reflect decision criteria located at different positions along the strength continuum (Donaldson, 1996; Dunn, 2004). On the basis of such models, one might expect some recognition-sensitive regions to demonstrate activity that varied in a linear fashion with putative memory strength. In contradiction to this expectation, we failed to detect any regions that showed this pattern of activity (either $R2 > R1 > K > M$, or vice versa), even at liberal significance thresholds. Of course, this null result does not constitute direct evidence against single-process models. It is however consistent with the results of a prior study in which regions where activity was graded as a function of rated familiarity (operationalized by recognition confidence) showed essentially no overlap with regions where activity differentiated recollected and highly familiar test items (Yonelinas et al., 2005; although see the caveat below concerning 'parametric analyses').

The present findings are inconsistent with those of Gonsalves et al. (2005), who investigated the neural activity elicited by test items in a face recognition memory test employing a conventional Remember/Know procedure. The authors reported three medial temporal regions (left parahippocampal, and left and right perirhinal cortices) in which activity was inversely correlated with increasing memory strength. We were unable to replicate these findings in our original analysis that searched for regions where activity declined with increasing memory strength, as well as in an additional analysis that employed the same recognition judgments as Gonsalves et al. (2005; i.e., CR, Miss, K and R, although this analysis did identify one small region in left prefrontal cortex where activity increased with increasing memory strength).

There are several plausible reasons for the disparity between these prior findings and the present results, including differences in experimental procedures and subjects' decision criteria (for example, false alarm rates were approximately 30% in Gonsalves et al. (2005), as opposed to 6% in the present case). Also relevant is that, unlike the present study, Gonsalves et al. identified strength-sensitive activity with a linear regression approach (sometimes called a 'parametric' analysis) that did not require activity levels associated with the different classes of recognition response to significantly differ from one another. Indeed, in the two perirhinal regions they identified as exhibiting strength effects, the magnitude of the activity elicited by items attracting correct rejections and misses was equivalent, in contrast to what would be predicted by a strength account. It is because parametric analyses do not uniquely identify strictly linear trends that we elected to employ the more conservative approach of inclusively masking the outcomes of sequential contrasts (see Results). A parametric analysis of our data ($p < 0.001$ with a 9 voxel extent threshold) along the lines of that performed by Gonsalves et al. (2005) revealed 12 clusters, totaling more than 4000 voxels, where activity seemingly increased in concert with increasing memory strength (i.e., from CR to R). The complementary analysis identifying regions where activity apparently diminished with increasing strength revealed a further 6 clusters, comprising more than 200 voxels. Inspection of Figure 5 illustrates that such analyses can be highly misleading if it is assumed that the regions that are identified will necessarily exhibit a linear trend across different experimental conditions. In both of these analyses, many of the voxels identified exhibited markedly non-linear patterns of activity that are inconsistent with the predictions of a strength-based account of recognition judgments.³ Thus, the outcome of a parametric analysis is not diagnostic with respect to hypotheses predicting that activity will vary linearly across experimental conditions. All this notwithstanding, it is noteworthy that our parametric analyses failed to identify any voxels within the medial temporal lobe where

activity was parametrically modulated by memory strength, even at a statistical threshold of $p < 0.05$. Thus, we were unable to replicate the findings of Gonsalves et al. (2005).

In contrast to our failure to identify a neural correlate of memory strength, we found several cortical regions where BOLD activity dissociated recollection and familiarity. Several of these regions - notably left inferior parietal cortex, superior prefrontal cortex, and left hippocampus in the case of recollection, and left superior parietal and anterior prefrontal cortex in the case of familiarity - accord well with those identified by Yonelinas et al. (2005). The recollection-sensitive parietal region also overlaps with the region implicated in recollection in other studies (Henson et al., 1999; Wheeler and Buckner, 2004; Woodruff et al., 2005; Vincent et al., 2006).

Unique among fMRI studies of recollection, the present study employed a procedure allowing recollection judgments to be segregated according to the amount of the information retrieved from the study episode. The rationale for the procedure rests on the assumption that whereas an R2 judgment depended on retrieval of a sufficiently detailed representation of the study episode to permit recovery of the test item's pairmate, an R1 response could be made on the basis of only partial retrieval of the encoding episode (instructions emphasized that recollection of only a single episodic detail was sufficient to justify an R1 response). We therefore assume that, on average, R2 judgments were associated with recollection of more information than R1 judgments, permitting identification of regions sensitive to amount of information recollected. Consistent with this assumption, we failed to identify any recollection-sensitive regions where activity was greater for R1 than R2 responses; if the information supporting R1 and R2 judgments differed in kind rather than in degree, such regions should have been evident.

In light of the results of our prior ERP study (Vilberg, Moosavi, and Rugg, 2006), we predicted that left inferior parietal cortex would be one of the regions sensitive to amount of information recollected (see Introduction), a prediction that was confirmed (Figure 4 and Table 4). This finding helps adjudicate among current ideas about the role of the parietal cortex in recollection. Two main suggestions have been made in this regard (see Wagner et al., 2005; Rugg and Henson, 2002; Wilding and Rugg, 1996). One possibility is that the region supports or operates upon representations of recollected information, perhaps acting as an 'episodic buffer' (Baddeley, 2000). An alternative notion is that activity in this region reflects a process that is triggered by the occurrence of recollection, but which does not support or operate on the retrieved information. An example of such a process is the modality-independent, temporoparietally localized 'circuitbreaker' proposed to initiate attentional shifts (Astafiev et al., 2006). Whereas both proposals predict greater left inferior parietal activity for recollected test items relative to those recognized on the basis of familiarity alone, it is arguable that only the former proposal predicts that activity will vary with amount of information retrieved. By this argument, therefore, the present findings conflict with an 'orienting' account of the role of the left inferior parietal cortex in recollection.

Left fusiform cortex, another region where recollection-related activity was greater for R2 than R1 judgments, is also worthy of comment. The area demonstrating this effect overlaps with regions previously implicated in visual object processing (e.g., Ishai et al., 1999; Bar et al., 2001), raising the possibility that recollection-related activity in this area reflects a role in the representation of retrieved information about the studied objects (cf. Vaidya et al., 2002; Wheeler and Buckner, 2004; Woodruff et al., 2005). The greater activity associated with R2 judgments is consistent with this proposal; presumably, the neural resources required to

³The reason for this is that the null hypothesis for across-subjects parametric analyses posits that the mean of a sample of regression coefficients does not differ from zero. Thus, so long as the coefficients demonstrate a consistent trend across subjects, the null hypothesis will be rejected regardless of the magnitude of the coefficients, and hence regardless of the amount of variance accounted for by a linear function.

represent two recollected objects are greater than the resources required to represent a single object.

The foregoing discussion implies that two distinctions can be drawn between recollection-sensitive cortical regions. The first is between regions that are sensitive to the amount of information retrieved (such as left inferior parietal cortex) and those that are not (prefrontal cortex, for example). Whereas caution must be exercised before accepting a null result (some or all of the regions identified as insensitive to amount recollected may of course turn out to respond to a more powerful manipulation) this distinction might be used to motivate a separation between recollection-sensitive effects that reflect processes supporting or operating on representations of retrieved information, and pre- or post-retrieval processes that operate in service of the recovery and utilization of retrieved information. These latter processes might include operations that successfully link a retrieval cue to a memory representation, as well as those that trigger attentional orienting toward the products of successful retrieval.

The present findings also point to a distinction between regions that are sensitive to amount of information recollected. In the present case, one such region - left fusiform cortex - is held to support the processing of high-level, but modality-specific information (visual object information). As noted, a plausible explanation for the recollection-related activity observed in this region is that it reflects the 'cortical reinstatement' of encoded objects (cf. Vaidya et al., 2002; Wheeler and Buckner, 2004; Woodruff et al., 2005), the activity varying in proportion to amount of information reinstated. By contrast, activity in the other principal region to demonstrate sensitivity to amount of recollected information - left inferior parietal cortex - appears not to be tied to a single sensory modality or type of information. Retrieval-related activity in this region occurs regardless of whether study and test materials are visual or auditory (Shannon and Buckner, 2004; Sohn et al. 2005), or whether the materials are pictorial (as in the present study), or verbal (e.g., Henson et al., 1999; 2005). Thus, if parietal cortex does indeed participate in the representation of recollected information, the representations seem likely to be coded at a supra-modal level of abstraction.

Finally, the question arises whether the present findings, which suggest that recollection-sensitive regions are modulated by amount of retrieved information, speak to the debate whether recollection is based upon a continuously varying or a thresholded memory signal (Wixted, 2007; Rotello et al., 2005; Yonelinas, 1994). The present study was of course predicated on the assumption that the information associated with the phenomenal experience of recollection can vary in a quantitative manner, and we have argued above that the findings support this assumption. Thus, our findings are inconsistent with an account of recollection (one that to our knowledge has no proponents) that posits that retrieval of information about a prior episode is 'all-or-nothing'. The findings do not however address the issue that is the focus of the current debate, namely, whether the information that supports the phenomenal experience of recollection *per se*, as operationalized by a 'Remember' judgment, is graded or thresholded.

Conclusions

The current findings provide further evidence that neural populations supporting recollection- and familiarity-driven recognition memory can be doubly-dissociated. Among the regions selectively sensitive to recollection, a subset are also sensitive to the amount of information recollected. One such region is left inferior lateral parietal cortex, raising the possibility that this region contributes to the representation or maintenance of recollected information.

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Figure 1.
Examples of stimuli used in the study and test phases.

Figure 2.

Regions selectively sensitive to recollection and familiarity. Familiarity-sensitive regions included the (a) left intraparietal sulcus, (c) left caudate nucleus, and (e) right precuneus. Recollection-sensitive regions included the (b) left precuneus/cuneus, (d) right caudate nucleus, and (f) left anterior medial temporal cortex. Left-hemisphere cortical effects are mapped onto inflated fiducial brains (see Methods). Sagittal sections are based on normalized across-subject mean anatomical images.

Figure 3. Bilateral hippocampal regions showing greater BOLD response for items afforded R2 than K judgments. Image thresholded at $p < 0.01$ (exclusively masked by $K > \text{Miss}$ at $p < 0.05$). Activity is illustrated on normalized across-subject mean anatomical images.

Figure 4.

Recollection-sensitive regions in the left hemisphere showing sensitivity to amount of information retrieved. Yellow regions are specifically sensitive to recollection (survive exclusive masking with $K > M$). Green regions are a subset of those recollection-sensitive regions in which activity increased with the amount of information recollected ($R2 > R1$). Identified regions included the (a) left inferior lateral parietal cortex and (b) left fusiform gyrus. Graphs show mean parameter estimates (and standard errors) of activity in the peak voxels of these two regions.

Figure 5.

Graphs show mean parameter estimates (and standard errors) of activity in the peak voxels of selected regions showing parametric increases (a and b) and decreases (b and c) in activity according to response category (Remember hits = R, Know hits = K, Misses = M, and Correct Rejections = CR). MNI coordinates of the regions are: (a) -3 33 27, (b) -3 -75 39, (c) -42 0 -9, and (d) 0 9 18.

Table 1
Proportions of Old and New Items Attracting R2, R1, K, and New Responses

Item	R2	R1	K	New
<i>Experiment 1</i>				
Old	.25	.29	.25	.17
New	.00	.02	.05	.90
<i>Experiment 2</i>				
Old	.19	.26	.26	.25
New	.00	.01	.04	.91

Note: Rows do not sum to 1.00 due to exclusion of response omissions.

Table 2

Test RTs (msec) for Experiments 1 and 2

RC	Experiment 1 (SD)	Experiment 2 (SD)
R2 Hit	1692 (259)	1577 (235)
R1 Hit	1716 (315)	1659 (208)
K Hit	1732 (334)	1625 (195)
CR	1224 (222)	1202 (183)
Miss	1451 (254)	1311 (181)

RT = Response time. RC = Response category. CR = Correct rejection.

Table 3
Cortical Regions Selectively Sensitive to Familiarity and Recollection

Region	BA	Location	Peak Z (# vox)
<i>Regions selectively sensitive to familiarity</i>			
L Middle Frontal Gyrus	11	-30, 48, -12	4.50 (30)
L Middle Frontal Gyrus	10	-30, 45, 27	3.70 (13)
L Middle Frontal Gyrus	10/46	-45, 39, 12	4.87 (24)
L Inferior Frontal Gyrus	44/45/46	-54, 21, 18	4.33 (56)
L Middle Frontal Gyrus	6/9	-48, 3, 39	3.66 (11)
R Middle Frontal Gyrus	6	24, 3, 51	3.39 (10)
R Claustrum	13	27, 6, 18	3.61 (12)
L Caudate Nucleus	---	-9, 0, 15	3.53 (14)
L Precentral Gyrus	6	-27, -15, 60	3.47 (14)
L Middle Temporal Gyrus	21/22	-66, -36, -3	3.89 (19)
L Inferior Parietal Lobe	2/40	-39, -30, 45	3.93 (20)
L Inferior Parietal Lobe	7/40	-30, -63, 45	4.80 (106)
R Inferior Parietal Lobe	40	42, -42, 36	3.90 (24)
R Inferior Parietal Lobe	40	33, -54, 45	3.74 (11)
R Superior Parietal Lobe	7	15, -72, 60	3.55 (14)
R Precuneus	7/31	6, -66, 30	3.40 (14)
<i>Regions selectively sensitive to recollection</i>			
L Superior Frontal Gyrus	8/9	-18, 33, 51	4.35 (48)
L Middle Frontal Gyrus	9	-48, 27, 33	3.85 (13)
L Superior/Middle Frontal Gyrus	6/8	-36, 21, 51	4.37 (70)
R Precentral Gyrus	4/6	36, -27, 69	3.60 (10)
R Caudate Nucleus	---	6, 9, -3	4.56 (34)
L Anterior Medial Temporal Cortex	34/37	-15, -3, -15	3.62 (16)
L Inferior Temporal Gyrus	20/21	-36, -9, -36	3.97 (18)
L Fusiform Gyrus	20/37	-51, -57, -21	4.12 (33)
L Fusiform Gyrus	18/19	-24, -87, -21	3.90 (9)
R Fusiform Gyrus	20/36	30, -33, -21	3.73 (9)
R Superior Parietal Lobe	7	33, -60, 57	3.64 (9)
L Parietal/Occipital Cortex	39/19	-36, -78, 33	5.10 (166)
L Cuneus/Precuneus	7/19	-9, -78, 33	3.93 (30)

Z values refer to peak activated cluster. L: left. R: right. BA = Brodmann area.

Table 4

Recollection-sensitive regions which are also sensitive to amount of information recollected

Region	BA	Location	Peak Z (# vox)
R Precentral Gyrus	4/6	33, -24, 72	2.91 (10)
L Fusiform Gyrus	30/37	-54, -54, -24	3.29 (25)
L Parietal/Occipital Cortex	19/39	-39, -81, 39	3.35 (54)

Z values refer to peak activated cluster. L: left. R: right. BA = Brodmann area.