



Task relevance modulates successful retrieval effects during explicit and implicit memory tests

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ABSTRACT

The *successful retrieval effect* refers to greater activation for items identified as old compared to those identified as new. This effect is particularly apparent in the ventral posterior parietal cortex (vPPC), though its functional properties remain unclear. In two experiments, we assessed the activation for old and new items during explicit and implicit tests of memory. In Experiment 1, significant effects were observed during explicit recognition performance and during an implicit lexical decision task. In both tasks, determining mnemonic status provides relevant information to task goals. Experiment 2 included a second implicit task in which determining mnemonic status was not relevant (color discrimination task). In this case, vPPC activation did not distinguish between old and new items. These findings suggest that automatic or implicit processes can drive retrieval-related activation in the vPPC, though such processes are gated by stimulus relevancy and task goals.

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Introduction

In functional neuroimaging studies of episodic memory, the activity in the posterior parietal cortex (PPC) is strongly correlated with successful retrieval. Specifically, PPC activity during retrieval is greater for items recognized as old (hits) compared to items recognized as new (correct rejections) (Konishi et al., 2000). This often left-lateralized retrieval-related activity, known as the *successful retrieval effect*, has been observed using a variety of study materials and test conditions (for review see Cabeza, 2008; Vilberg and Rugg, 2008; Wagner et al., 2005). Additional findings suggest a functional-anatomical dissociation within PPC regions, such that the activity in the ventral regions (vPPC: supramarginal gyrus, temporal-parietal junction, and angular gyrus) correlates with recollective responses, whereas the activity in the dorsal regions (dPPC: intraparietal sulcus and superior parietal lobule) correlates with weaker familiarity responses (Wheeler and Buckner, 2004).

Several models characterize the role of the PPC in episodic retrieval (Wagner et al., 2005). The *episodic buffer* model suggests that the vPPC serves as a multi-modal buffer in which the retrieved features of an episodic memory are held online for further processing (Vilberg and Rugg, 2007, 2008). In this model, the vPPC activity is presumed to index the amount of information retrieved. Alternatively, an atten-

tional account has been put forth and described as the *Attention to Memory hypothesis (AtoM)* (Cabeza, 2008; Ciaramelli et al., 2008). This model draws on the finding that an analogous dorsal-ventral dissociation exists in selective attention to visual stimuli such that voluntary, goal-directed attention drives the dPPC activity and involuntary, stimulus-driven attention drives the vPPC activity (Corbetta and Shulman, 2002). Applying this model to episodic retrieval, AtoM suggests that the dPPC initiates and carries out effortful, top-down memory searches while the vPPC monitors the output from the medial temporal lobe, activating in response to the relevant output and signaling the need to redirect attention towards this information.

The extant research on the role of the PPC in episodic memory has focused on explicit retrieval. It is not clear to what extent this region is involved when previously studied items are encountered in the absence of directed or intentional retrieval, which we term implicit retrieval. If the vPPC is fulfilling a stimulus-driven role, whether temporarily storing or signaling the presence of unattended memory traces, one might expect activation in this region to occur even when retrieved information is accessed in an automatic or implicit manner. By this view, the relevance of stimulus features to task goals may play a significant role in driving PPC responses. Research on the neural basis of selective attention has shown that relevant stimuli appearing in unattended locations captures attention and activates a fronto-parietal network that includes the vPPC. Yet the task irrelevant stimuli, even when salient, fail to engage this network (Downar et al., 2001; Indovina and Macaluso, 2007). Thus, it may be that the stimulus filtering occurs that prevents or reduces the vPPC activity (Shulman et al., 2007).

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We focus on the vPPC as its role in memory remains contested and this region appears to be susceptible to the effects of task relevance. In order to more directly assess the ventral components of the broader successful retrieval effect, we chose to employ contrasts characterizing the recollection-related activity (high confidence old responses compared to new items) when possible. While the attention-related activations mentioned previously are often right-lateralized, in contrast with the left-lateralized memory-related activations, this may be partly due to differences in stimulus features such as verbalizability rather than hard-wired hemispheric differences (Klostertmann et al., 2009). It is possible that the influence of the task relevance on vPPC activation occurs in both hemispheres and across task types. Our use of the term “task relevance” here refers to whether the mnemonic status of an item carries useful information towards providing a correct response. In the following experiments, we vary the task-relevance of mnemonic status in order to evaluate relative differences in activation for old and new items during explicit and implicit retrieval.

Experiment 1

We assessed the *successful retrieval effect* during explicit yes/no Recognition and during an implicit Lexical Decision (LD) task. In the LD task, participants simply determined if a test item was a word or non-word. Half of the words were previously presented as study items and the other half were new words. In the cross-task analyses, we compared the influence of old vs. new words for both lexical decisions and recognition memory.

Methods

Participants

Twenty-one healthy subjects participated in this study (mean age 22.05 years, range 19–34 years; 14 females). One additional subject was excluded from analysis due to excessive head motion and scanner artifact. All subjects were paid for their participation and gave informed consent according to the guidelines approved by the UC Berkeley Office for the Protection of Human Subjects. All subjects were native English speakers and were right-handed. None of the subjects reported a history of neuropsychiatric disorders, brain injury or having recently taken psychoactive medication.

Stimuli

Word and non-word stimuli were drawn from the English Lexicon Project database (<http://elexicon.wustl.edu/default.asp>). The entire stimulus set consisted of 280 words and 140 non-words. Words consisted of five to seven letters with an average HAL log word frequency of 6.45 ($SD = 1.30$). The non-words were five to seven letters long and constructed by generating 140 comparable words and altering them by randomly changing one letter to produce a unique non-word (e.g. HEPOR, SLISHTS). Non-words had an average bigram frequency of 1201 ($SD = 484.72$) and an orthographic neighborhood average of 1.45 ($SD = 0.97$). Words and non-words were divided into lists and rotated across conditions such that specific items used as study and test stimuli were counterbalanced across subjects.

Behavioral procedure

The study phase was conducted outside of the scanner. Subjects were presented 140 words divided into two blocks of 70 words each. Each study trial consisted of a central fixation cross (500 ms), a word (1500 ms), and a blank screen (1000 ms). For each word, subjects made pleasant/unpleasant judgments using a button box. They were not informed of the later memory tasks.

Approximately 20 min after the study session, subjects were placed into the scanner for the test phase. The two LD blocks always preceded the two recognition blocks to help reduce memory-related

retrieval strategies during the LD task. Subjects viewed the stimuli projected onto a screen at the end of the magnet bore using a mirror mounted over the head coil. The stimuli were presented using E-Prime software (Psychology Software Tools, Inc, Pittsburgh, PA; <http://www.pstnet.com>).

During the LD task, a total of 70 old words (i.e., words presented during the study phase), 70 new words, and 140 non-words were presented over two runs. A single LD trial consisted of a stimulus presentation (500 ms), a blank screen (1000 ms) and a jittered inter-trial interval during which a center fixation cross was presented ($ITI = 250\text{--}3750$ ms). Subjects were instructed to determine whether a stimulus was a word or non-word. Responses were made with either a left or right button press using the thumbs of each hand. The buttons corresponding to each response were counterbalanced across subjects.

During the Recognition task, 70 old words and 70 new words were presented over two runs. All words used during the Recognition task were different from those used in the LD task. A single recognition trial consisted of a stimulus presentation (750 ms), a blank screen (2250 ms) and a jittered ITI (500–4000 ms) during which a central fixation cross was displayed. Subjects were instructed to judge whether a word was old or new and to give a simultaneous confidence rating of their answer. Subjects were instructed to use the high confidence answers only if they were 100% sure of their response. Responses could be made during either the stimulus presentation or blank screens. The thumbs of both hands were used to make the responses (“HC-Old”, “LC-Old”, “LC-New”, “HC-New”) on a four-button response box. The buttons corresponding to each choice were counterbalanced across subjects. Response times and accuracy were recorded.

fMRI acquisition

Subjects were scanned in a 3T Siemens (Erlangen, Germany) Trio scanner at the UC Berkeley Brain Imaging Center. Each of the 4 runs acquired used a T2*-weighted echo-planar imaging (EPI) sequence [$TR = 1750$ ms; $TE = 22$ ms; flip angle = 90° ; matrix = 128×128 ; FOV = 220 mm; 3 mm slice thickness] with GRAPPA [acceleration factor 3]. 32 axial slices oriented to the AC–PC were acquired in an interleaved order giving whole brain coverage. 216 volumes were collected during each of the two LD runs and 182 volumes were collected during each of the recognition runs. The first 5 volumes of each run were to allow for magnetization preparation. A high resolution magnetization-prepared rapid-acquisition gradient echo (MPRAGE) [$TR = 2300$ ms; $TE = 2.98$; matrix = 256×256 ; FOV = 256; sagittal plane; slice thickness = 1 mm; 160 slices] and a gradient-echo multislice (GEMS) [$TR = 250$ ms; $TE = 22$; matrix = 256×256 ; FOV = 256; 3 mm slice thickness, 32 slices] were collected for registration purposes.

fMRI data analysis

Data were preprocessed and analyzed with the FSL toolbox v4.1.4 (<http://www.fmrib.ox.ac.uk/fsl>; Smith et al., 2004). Motion correction was performed with MCFLIRT, aligning all images to the middle slice with rigid body transformation. Slice timing correction was performed using (Hanning windowed) sinc interpolation to shift each slice in the volume in reference to the middle of the TR period. BET (brain extraction tool) was then used to create a mask of the brain from the first volume of each time series and used to separate the brain from the surrounding skull and tissue in each volume. All images were spatially smoothed with a 5 mm FWHM Gaussian kernel to reduce noise. High pass temporal filtering was performed using the local Gaussian-weighted fit of a running line to remove low frequency artifacts. Subject data was registered to standard space in a two-step process using FLIRT (FMRIB's Linear Image Registration Tool). First, EPIs were registered to each subject's skull-stripped high resolution T1-weighted image. Second, subject's T1-weighted images were

registered to standard (MNI) space (FSL's MNI152 template). The two registrations were then combined to take the subject's EPI images and run-level statistical maps into standard space.

A multi-level, mixed effects general linear model was run using FILM (FMRIB's Improved Linear Model) which treated subjects as random effects. Individual runs were modeled in subject space and the resulting statistical maps were registered to standard space for higher level analysis. Regressors of interest were obtained by convolving stimulus onset times with FSL's canonical (gamma) hemodynamic response function and their temporal derivative. Motion parameters were included as additional confound variables and temporal autocorrelation was removed through prewhitening. Trials with no response and incorrect trials were also modeled as regressors of no interest. Contrasts were entered to compare old vs. new status, words vs. non-words, and high confidence vs. low confidence responses.

A second level analysis combined the runs for each subject using a one-sample *t*-test, treating runs as fixed effects. Third-level group statistics maps were created for each contrast using FLAME (FMRIB's Local Analysis of Mixed Effects). FLAME implements a Bayesian two-stage model, the first being a fast approach to the posterior probabilities of activation for each voxel and the second uses a slower Markov Chain Monte Carlo (MCMC) based analysis for all voxels identified as being near the threshold in the first stage. The whole brain family-wise error was corrected to $P < .05$ using the Gaussian Random Field theory with a cluster forming threshold of $z > 2.3$. For visualization purposes, results from these analyses were rendered on inflated brains using the CARET software (<http://www.nitrc.org/projects/caret/>).

As a follow-up analysis to assess further the cross-task results, we conducted an ROI analysis in order to perform an ANOVA on the percent change of the peak parameter estimates using Task (Recognition/LD) and Condition (old/new) as factors. Parameter estimates were extracted from a region defined by inclusively masking the contrasts demonstrating the *successful retrieval effect* (old > new) in both the Recognition and LD tasks. We used the clusters produced from the whole brain analysis, thus each was individually thresholded at a level of $p < .05$, corrected.

Results

Behavioral results

Recognition task. The mean hit rate was 85% with a correct rejection rate of 81%. Reaction times were significantly faster for old items (mean = 1229 ms) than new items (mean = 1382 ms), $t(20) = 3.917$, $p < .001$. Memory performance (hit rate) was significantly better for the HC responses compared to the LC responses, 90.4% vs. 72.3% $t(20) = 13.601$, $p < .001$. HC responses (mean = 1212 ms) were also faster than LC responses (mean = 1606 ms), $t(20) = 5.846$, $p < .001$.

Lexical decision task. Subjects correctly identified words and non-words at a similar rate, 93.6% vs. 92.4%, $t(20) = 1.05$, $p = 0.31$. For words, old items were correctly identified better than the new items, 95.2% vs. 89.7%, $t(20) = 3.943$, $p < .001$. Subjects responded faster on correct Word judgments (mean = 690 ms) than they did to correct non-word judgments (mean = 720 ms), $t(20) = 3.455$, $p < .01$. Examining words only, responses for old items (mean = 683 ms) were significantly faster than the new items (697 ms), $t(20) = 2.383$, $p < .05$.

fMRI Results

Recognition task. Consistent with the previous studies (Cabeza et al., 2008; Vilberg and Rugg, 2008; Wagner et al., 2005), HC-Old items activated a neural circuit that included the prefrontal cortex, parietal cortex, and the medial temporal lobe (see Table 1 for full results).

Table 1
Experiment 1 regions active during Recognition task for correct HC-Old > CR contrast.

Region	Hemisphere	X (mm)	Y (mm)	Z (mm)	Z-score
Lingual gyrus	R	30	-38	-12	3.07
Parahippocampal gyrus	R	22	-20	-16	3.07
	R	30	-28	-14	3.39
	R	28	-34	-12	3.03
Parahippocampal gyrus	L	-28	-42	0	3.66
Hippocampus	R	28	-22	-16	3.33
Hippocampus	L	-24	-28	-8	3.38
Hippocampus	L	-20	-22	-10	2.89
Temporal occipital fusiform cortex	R	28	-44	-12	3.01
Thalamus	L	-14	-36	6	2.93
Inferior temporal gyrus	L	-52	-40	-14	3.22
	L	-52	-36	-14	3.18
	L	-48	-42	-12	3.1
Middle temporal gyrus	L	-58	-42	-6	4.27
	L	-56	-22	-14	3.2
	L	-54	-28	-12	3.16
Frontal orbital cortex	L	-26	30	-14	3.76
	L	-34	36	-10	3.67
	L	-26	18	-12	3.34
Frontal pole	L	-34	16	-18	3.08
	L	-30	38	-12	2.99
	R	46	-12	14	3.34
Central opercular cortex	R	58	-10	12	3.31
	R	48	-4	8	3.28
	R	56	-6	12	3.2
Parietal operculum cortex	R	56	-32	22	3.37
	R	58	8	8	3.31
	L	-50	-52	38	4.09
Angular gyrus	L	-50	-56	30	3.49
	L	-40	-72	36	4.6
	L	-46	-62	36	4.17
Lateral occipital cortex	L	-44	-68	30	3.9
	L	-32	-74	42	3.77
	L	-4	-48	30	5.05
Posterior cingulate gyrus	L	-4	-38	32	4.42
	L	-6	42	8	3.79
	L	-2	-54	28	4.24
Precuneus cortex	L	-6	-66	24	4.63
	L	-10	-58	20	4.2
	L	-14	-60	14	4.14
Anterior cingulate	L	-10	38	2	3.74
	L	-16	54	18	3.93
	L	-4	58	10	3.73
Paracingulate gyrus	L	-4	54	-2	4.08
	L	-6	50	14	3.93

Specifically, we observed increased activation for HC-Old responses compared to the new responses in the left vPPC, left frontal pole extending into the left dorsolateral prefrontal cortex (DLPFC), bilateral posterior cingulate, bilateral precuneus and the left posterior hippocampal complex (Fig. 1a). Additional activations were seen in the left orbitofrontal cortex (OFC), left middle temporal gyrus, and right parietal operculum. The contrast of all old items that collapsed across the HC and LC judgments to the new items yielded similar results, with the exception of the left orbitofrontal, middle temporal gyrus and hippocampal clusters.

Lexical decision task. With respect to the basic lexical decision contrast (words vs. non-words), our findings were comparable to those observed in the previous studies (Henson, 2002; Mummery et al., 1999; Rossell et al., 2001). A primarily left lateralized language network was activated for words > non-words, which included the left middle temporal gyrus, left vPPC extending superiorly into the inferior parietal sulcus, left OFC, left middle and superior frontal gyrii, and anterior cingulate extending into the frontal poles. There was also bilateral precuneus and posterior cingulate activation (see Table 2 for full list of results).

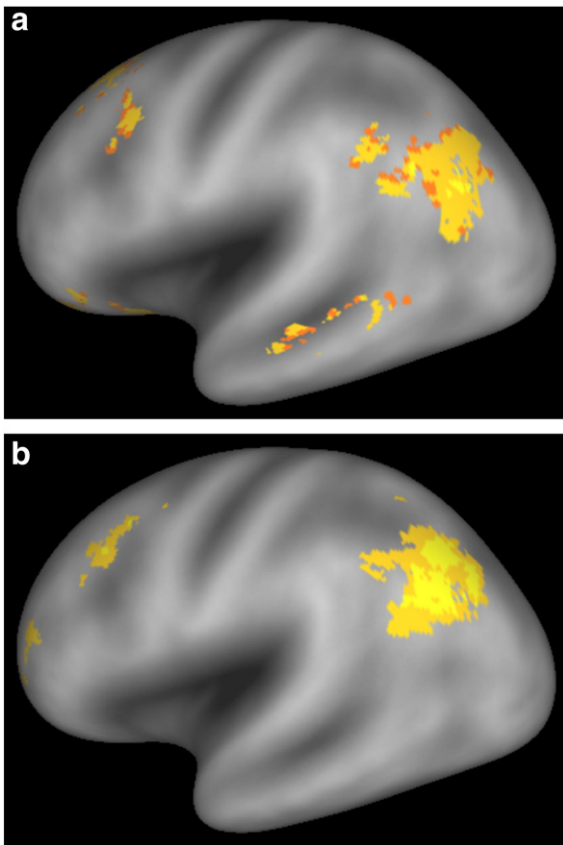


Fig. 1. Experiment 1: a) regions active during Recognition task for correct HC-Old > New contrast. b) Regions active during LD task for correct old word > new word contrast. Threshold at $P < .05$, corrected.

We were particularly interested in the contrasts between the old vs. new words presented during the LD task as in this task explicit episodic retrieval is not required. A contrast of old words > new words revealed a similar pattern of activation in the PPC as was observed in

Table 2
Experiment 1 regions active during LD task for correct word > non-word contrast.

Region	Hemisphere	X (mm)	Y (mm)	Z (mm)	Z-score
Middle temporal gyrus	L	-58	-48	6	4.55
	L	-56	-44	-6	4.06
	L	-56	-38	-6	4.04
	L	-62	-28	-6	3.18
Superior temporal gyrus-anterior division	L	-52	-38	-2	3.1
	L	-50	-8	-16	3.38
Lateral occipital cortex	L	-32	-68	36	4.49
	L	-34	-64	44	4.45
	L	-40	-64	42	4.38
	L	-46	-62	22	4.37
Angular gyrus	L	-46	-60	28	4.12
	L	-54	-48	32	4.12
Posterior cingulate	L	-6	-40	38	4.64
	L	-2	-36	28	4.46
	L	0	-46	22	4.29
	L	-2	-74	34	4.02
Precuneous cortex	L	-2	-72	28	3.92
	L	-6	-80	42	3.8
	L	-8	54	12	3.85
	L	-26	14	54	3.79
Paracingulate gyrus	L	-26	38	-10	3.78
	L	-12	56	24	3.7
	L	-12	54	28	3.69
	L	-36	42	12	3.68

the Recognition task. Specifically, we found significant activation in the bilateral vPPC, precuneus, and posterior cingulate gyrus (Fig. 1b). Additionally, we observed activation in the left middle frontal gyrus and a small cluster in the left lateral frontal pole (see Table 3 for the full list of results). However, the more medial frontal activations that were present during the Recognition task (anterior cingulate and OFC) were absent during the LD task. These activations will be discussed later with respect to implicit memory processes.

Cross-task analyses

We performed analyses across the Recognition and LD tasks as a way to examine differences between activations during explicit (Recognition task) and implicit (LD task) retrieval. A direct comparison of the successful retrieval effect (contrast of [HC-Old > New_Recognition] vs. [Old > New_LD]) revealed no difference in the vPPC activation. The areas that did demonstrate a greater old/new effect during the Recognition task included: the left middle temporal gyrus, left DLPFC, left hippocampus, anterior cingulate and posterior cingulate, and lateral occipital cortex (see Table 4 for the full list of results).

The ROI used for follow-up analysis was derived by inclusively masking the old > new contrasts from the above analysis of the Recognition and LD tasks to produce a cluster of common activation. The resulting ROI from which a percent change of peak parameter estimates were extracted fell within the left vPPC, specifically the angular gyrus ($x = -47$, $y = -55$, $z = 37$; 104 voxels). Further illustrating the lack of difference between the magnitude of the old/new effect between tasks, the Task \times Condition interaction was not significant, $F(1,20) = 1.02$, $p = .33$ (Fig. 2). However, the main effects of Task [$F(1,20) = 8.98$, $p < .01$] and Condition [$F(1,20) = 12.9$, $p < .01$] were significant. Old items showed greater activation in the Recognition task than the LD task [$t(20) = 2.68$, $p < .01$], a finding that might be explained by the fact that more information is retrieved

Table 3
Experiment 1 regions active during LD task for correct old word > new word contrast.

Region	Hemisphere	X (mm)	Y (mm)	Z (mm)	Z-score
Angular gyrus	R	42	-54	48	3.04
	R	38	-68	44	3.15
Lateral occipital cortex	R	42	-62	42	3.46
	L	-20	58	6	3.07
Frontal pole	L	-24	56	6	3.11
	L	-36	42	14	3.17
	L	-26	54	2	3.18
	L	-24	50	-2	3.23
	L	-28	54	-2	3.29
	L	-34	10	50	2.97
Middle frontal gyrus	L	-34	10	40	3.07
	L	-34	6	42	3.15
	L	-40	14	44	3.19
	L	-38	8	50	3.2
Posterior cingulate	L	-38	14	40	3.5
	L	-2	-42	36	2.94
	L	-4	-46	22	3.43
Posterior cingulate	L	-4	-30	30	3.56
	R	2	-42	24	3.2
Precuneous cortex	R	6	-40	22	3.52
	L	-4	-66	38	3.4
	L	-4	-66	20	3.43
	L	-6	-64	30	3.57
Precuneous cortex	L	-6	-72	30	3.81
	R	8	-66	26	3.4
	R	2	-66	34	3.43
Lateral occipital cortex	L	-42	-62	36	3.75
	L	-40	-64	32	3.85
	L	-38	-68	42	4.04
	L	-34	-74	38	4.18
	L	-34	-66	48	4.26
	L	-44	-60	42	4.32

Table 4
Experiment 1 regions active during cross-task analysis of [HC-Old>New_Recognition]> [Old word>New word_LD].

Region	Hemisphere	X (mm)	Y (mm)	Z (mm)	Z-score
Postcentral gyrus	R	28	−32	56	3.22
	R	28	−34	60	2.93
Precentral gyrus	R	36	−24	64	3.47
	R	24	−20	52	3.14
Caudate	L	−8	12	4	2.95
Caudate	R	8	8	12	3.18
	R	8	6	0	2.98
Nucleus accumbens	L	−10	16	−4	3.35
Lateral occipital cortex	R	36	−82	10	3.22
	R	30	−86	24	3.13
	R	32	−86	12	3.02
	R	26	−86	24	3.01
	R	36	−88	6	2.86
Lateral occipital cortex	L	−38	−74	18	3.7
	L	−38	−66	26	3.44
	L	−40	−70	28	3.36
	L	−28	−84	8	3.25
	L	−44	−72	24	3.03
	L	−40	−72	34	2.99
Occipital pole	R	24	−94	14	3
Middle temporal gyrus	L	−56	−48	0	3.95
	L	−58	−42	−8	3.44
	L	−48	−22	−14	3.43
	L	−56	−24	−10	3.35
	L	−52	−32	−12	3.23
	L	−58	−22	−16	3.16
Central opercular cortex	R	46	−12	18	3.62
Insular cortex	R	30	−24	20	3.26
Parietal operculum cortex	R	34	−22	20	3.36
	R	46	−24	24	3.29
	R	40	−24	16	3.22
Precentral gyrus	R	58	6	8	3.74
Frontal orbital cortex	L	−28	28	−12	3.63
	L	−34	36	−12	3.6
Frontal pole	L	−40	48	−2	3.4
Hippocampus	L	−22	−28	−6	3.68
	L	−20	−36	12	3.59
Lingual gyrus	L	−28	−60	−2	3.67
Posterior cingulate	L	−2	−46	34	4.14
	L	−6	−50	28	3.79
	L	−6	−42	32	3.77
	L	−2	−50	20	3.67
Precuneus cortex	L	−12	−58	14	4.01
	L	−10	−56	18	3.96
Anterior cingulate	L	−6	42	8	4.3
	R	2	38	6	3.94
Paracingulate gyrus	L	−4	54	−2	4.29
	L	−8	52	4	4.03
	L	−6	50	14	3.9
	L	−8	54	−4	3.88
Superior frontal gyrus	L	−24	26	48	3.21
Middle frontal gyrus	L	−30	16	52	3.39

as part of the explicit retrieval nature of the Recognition task. However, this would not necessarily explain why new items also showed greater activation in Recognition compared to the LD task, $t(20) = 2.78$, $p < .01$. If the vPPC activation indexes the amount of information retrieved, the two tasks should have similarly low levels of activation in response to the new items.

The findings from Experiment 1 demonstrate the similarities and differences between explicit and implicit retrieval. The successful retrieval effect was present during both tasks and while a main effect of task indicated higher activity for both conditions during Recognition, the difference between the old and new items was of similar magnitudes in each task. Additional activation occurred in the prefrontal areas during the Recognition task, which may represent control and monitoring processes accompanying explicit retrieval. We also found that old items produced greater vPPC activation in the Recognition task compared to the LD task. This finding may be

explained by some unintentional explicit retrieval occurring during the LD task, in which subjects cannot help but process and retrieve some information when encountering old items. The intentional retrieval occurring during the Recognition task would account for the higher level of activity in response to the old items. However, the same explanation does not account for the finding that new items show similarly elevated levels of activation in Recognition compared to the LD task. If the vPPC activation is simply an index of retrieved information, we would not expect heightened levels of activity to accompany new items during recognition. This led us to examine alternative explanations for these patterns of activity in a second experiment.

Experiment 2

The first experiment showed that the successful retrieval effect can be observed during implicit retrieval. One explanation for this finding is that the vPPC activity during the implicit task was simply a product of unintentional explicit retrieval and that the activation was a direct reflection of retrieved information. Yet, an alternative explanation is that the vPPC activity is actually an index of processing relevant stimulus information, in this case mnemonic status. Under this interpretation, vPPC activity would be evoked by any relevant output from the MTL, whether arising from bound representations that have been activated during the successful retrieval of old items or something akin to a novelty signal in response to the new items. In both the Recognition test and the LD task, the determination of mnemonic status facilitates goal-directed behavior. To assess this factor, we included a second implicit condition that diminished the relevance of processing mnemonic status. Though the presentation of old items would still induce similar levels of unintentional explicit retrieval as may be present in the LD task, the output of these retrieval processes held little task relevance. In this Color Discrimination (CD) task, participants simply determined whether a test item was red or green.

Methods

Participants

Twenty-seven healthy subjects participated in this study (mean age 21.44 years, range 18–28 years; 15 females). Two additional subjects were excluded from the analysis due to excessive head motion and poor behavioral performance. All subjects were paid for their participation and gave informed consent according to the guidelines approved by the UC Berkeley Office for the Protection of Human Subjects. All subjects were native English speakers and were right-handed. None of the subjects reported a history of neuropsychiatric disorders or brain injury or having recently taken psychoactive medication.

Behavioral procedure

Procedures for the study phase remained identical to Experiment 1 with the exception being that 210 words were presented over two blocks (105 words each).

At test, the LD and Recognition tasks used identical procedures as in Experiment 1 with some minor changes to trial timing. Additionally, a Color Discrimination task was added. Two blocks of each task were run, with the order of tasks randomized across subjects. During the LD task, the jittered inter-trial interval displaying a fixation cross was changed to 500–4500 ms. Recognition trial timings were also changed slightly such that each consisted of a stimulus presentation (500 ms), a blank screen (2500 ms), and a jittered ITI displaying a fixation cross (1000–5000 ms).

In the CD task, 70 old words and 70 new words were presented over two runs. Half of each word category was presented in red font and the other half in green font. A single CD trial consisted of stimulus

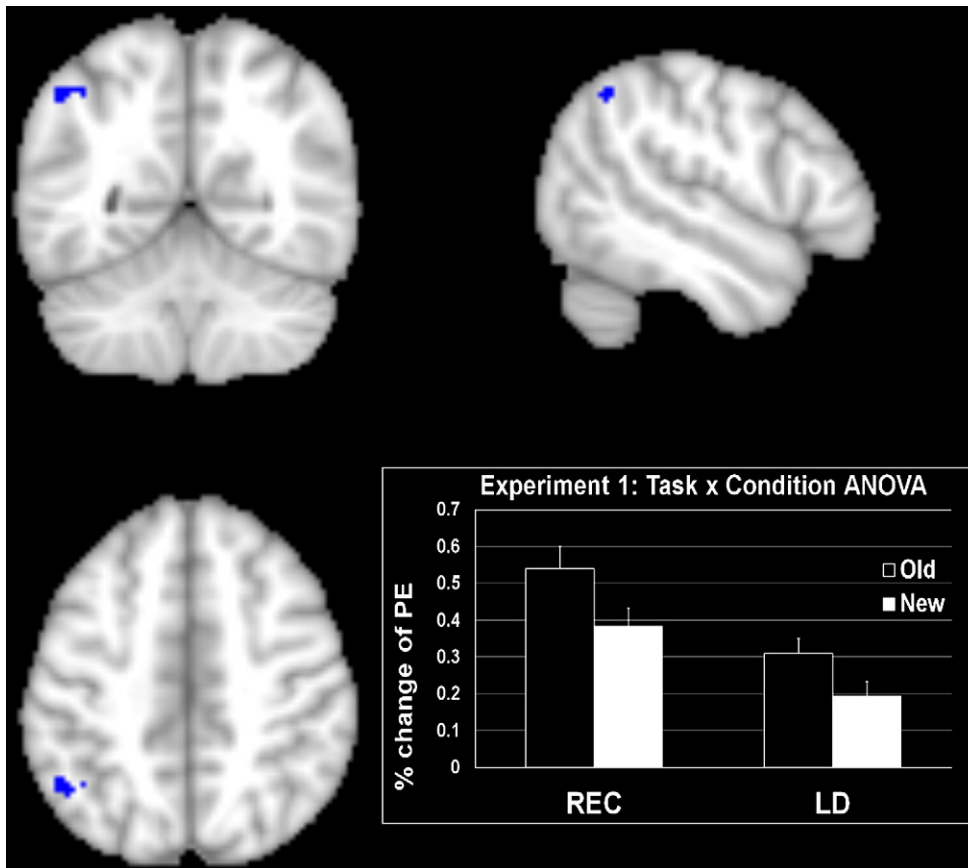


Fig. 2. Experiment 1: ROI derived from inclusively masking HC-Old>New_Recognition with Old word>New word_LD shown in blue. Bar chart displays percent change of peak parameter estimates extracted from ROI. There were significant main effects for condition and task, but no interaction.

presentation (500 ms), a blank screen (1000 ms) and a jittered inter-trial interval during which a center fixation cross was presented (ITI = 500–4500 ms). Subjects were instructed to determine whether a stimulus was printed in a red or green font. Responses were made with either a left or right button press using the thumbs of each hand.

fMRI acquisition

Scanning was conducted using the same procedure as in Experiment 1 except for some changes to the functional sequences described below. Each of the 6 runs acquired used a T2*-weighted echo-planar imaging (EPI) sequence [TR = 2000 ms; TE = 26 ms; flip angle = 90°; matrix = 128 × 128; FOV = 256 mm; 3 mm slice thickness] with GRAPPA [acceleration factor 4]. 37 axial slices oriented to the AC–PC were acquired in an interleaved order giving whole brain coverage. 224 volumes were collected during each of the two LD runs, 189 volumes were collected during each of the Recognition runs and 119 volumes were collected during each of the CD runs. Finally, the first 5 volumes of each run were removed to allow for magnetization preparation.

fMRI data analysis

Data analysis was conducted using the same procedure as in Experiment 1. For planned contrasts examining activation in our ventral PPC region of interest, we used a pre-threshold mask before correcting for multiple comparisons. This was defined as the angular gyrus mask in the Harvard-Oxford Cortical Structure Atlas. Additional results obtained from the non-masked, whole brain analysis are also reported.

Behavioral results

Recognition task. The mean hit rate was 85% with a correct rejection rate of 65%. Reaction time was significantly faster for the old items (mean = 1197 ms) than the new items (mean = 1564 ms), $t(26) = 8.296$, $P < .001$. Memory performance (correct–incorrect) was significantly better for the HC responses compared to the LC responses, $t(26) = 7.565$, $P < .001$. The HC responses (mean = 1210 ms) were also made significantly faster than the LC responses (mean = 1721 ms), $t(26) = 11.962$, $P < .001$.

Lexical decision task. Subjects were able to correctly identify (correct–incorrect) words and non-words at a similar rate, $t(26) = 0.29$, $P = 0.77$. When looking at just words, the old items were correctly identified (correct–incorrect) significantly better than the new items, $t(26) = 3.519$, $P < 0.01$. The subjects responded faster on correct word judgments (mean = 724 ms) than they did to correct non-word judgments (mean = 794 ms), $t(26) = 6.99$, $P < 0.001$. Examining words only, old items (mean = 712 ms) were responded to significantly faster than the new items (737 ms), $t(26) = 3.477$, $P < .01$.

Color discrimination task. Memory performance (correct–incorrect) for old and new words was similar, $t(26) = 0.246$, $P = 0.81$. There was also no difference in performance between red and green words, $t(26) = 0.092$, $P = 0.93$. Subjects responded with similar reaction times to old (mean = 523 ms) and new words (mean = 527 ms), $t(26) = 0.894$, $P = .38$. However, there was a significant difference in responses between green words (mean = 520 ms) and red words (mean = 531 ms), $t(26) = 2.072$, $P < .05$.

fMRI Results

Recognition task. The comparison of correct HC-Old items to the new items revealed activations similar to those in Experiment 1. Specifically, we observed increased activation for HC-Old responses compared to the new responses within the angular gyrus mask ($x = -42$, $y = -52$, $z = 48$). The global analysis revealed additional clusters in the left frontal pole extending into the left dorsolateral prefrontal cortex, left posterior cingulate and precuneus, and left middle temporal gyrus (Fig. 3a, see Table 5 for the full list of results). The contrast of all old items that collapsed across HC and LC judgments to the new items yielded similar results, with the exception of the right lateral occipital cortex, posterior midline, and anterior extent of the frontal pole clusters.

Lexical decision task. Our contrast of interest was to compare old words > new words. Within our angular gyrus mask, there was a significant cluster ($x = -42$, $y = -52$, $z = 46$ and $x = -46$, $y = -60$, $z = 48$) reflecting the successful retrieval effect (Fig. 3b). The global analysis did not produce any additional clusters that survived correction for multiple comparisons.

Color discrimination task. We next looked for the presence of the successful retrieval effect in the CD task in the case of activity being caused due to unintentional explicit retrieval. The contrast of old words > new words did not produce any significant clusters within the vPPC.

Cross-task analyses. We performed analyses across the three tasks in order to compare magnitudes of old vs. new differences during explicit retrieval (Recognition task), relevant implicit retrieval (LD

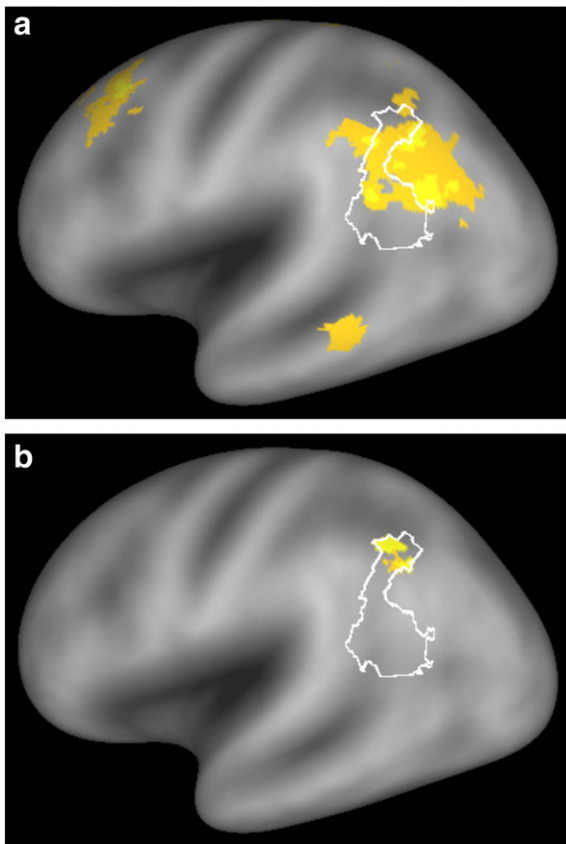


Fig. 3. Experiment 2: a) regions active during Recognition task for correct HC-Old > New contrast. b) Regions active during LD task for correct old word > new word contrast. Threshold at $P < .05$, corrected.

Table 5

Experiment 2 regions active during Recognition task for correct HC-Old > New contrast.

Region	Hemisphere	X (mm)	Y (mm)	Z (mm)	Z-score
Superior frontal gyrus	L	-2	40	56	4.73
	L	-4	30	62	4.44
	L	-22	22	62	4.21
	L	-8	16	70	4.17
	L	-10	26	50	4.08
Angular gyrus	L	-32	16	50	4.32
	L	-42	-58	48	4.03
	L	-52	-52	30	3.91
Lateral occipital cortex	L	-42	-62	28	4.14
	L	-46	-66	32	3.81
	L	-50	-68	26	3.78
	L	-42	-64	52	3.63
	L	-4	-88	46	3.62
Lateral occipital cortex	L	-12	-84	40	3.17
	L	-12	-86	34	3.12
	R	44	-86	4	3.38
Posterior cingulate	R	34	-76	2	3.33
	L	-2	-18	30	3.97
Precuneus cortex	L	0	-40	8	3.76
	L	-2	-30	34	3.55
	L	-2	-40	46	3.84
Cuneal cortex	L	-12	-54	24	3.55
	L	-10	-72	28	3.39
	L	-2	-76	38	3.08
Occipital pole	L	-10	-82	34	3.08
	R	32	-90	32	3.63
Occipital fusiform gyrus	R	34	-90	22	3.53
	R	30	-96	18	3.52
	R	36	-66	-8	3.53
Precentral gyrus	L	-10	-18	74	3.97
	L	-8	-18	50	3.92
Precentral gyrus	R	6	-14	58	3.54
	R	2	-34	66	3.44
Postcentral gyrus	L	0	-34	62	3.78
	L	-14	-32	78	3.45
	L	-60	-38	-6	3.51
Middle temporal gyrus	L	-68	-46	-12	3.44
	L	-64	-36	0	3.39
	L	-64	-50	-12	3.35
	L	-68	-42	-6	3.26
	L	-68	-30	-10	3.22

task), and irrelevant implicit retrieval (CD task). As in Experiment 1, there were no significant clusters where old vs. new effects were different between the Recognition and LD tasks ([HC-Old-New_Recognition] > [Old > New_LD]). When we directly compared old vs. new contrasts between Recognition and CD ([HC-Old-New_Recognition] > [Old > New_CD]), we found significant clusters within the angular gyrus mask ($x = -44$, $y = 48$, $z = 48$). Additionally, there were clusters in the left frontal poles extending into DLPFC, posterior cingulate, precuneus, and left inferior and middle temporal gyri (see Table 6 for the full list of results). Critically, the comparison of implicit old vs. new contrasts when mnemonic status was relevant vs. irrelevant ([Old > New_LD] > [Old > New_CD]) yielded a significant cluster within the angular gyrus mask ($x = -42$, $y = -56$, $z = 48$). Furthermore, the resulting cluster overlapped with the comparison of old > new contrasts between Recognition and CD in the angular gyrus (Fig. 4).

Discussion

In the two experiments, we assessed the influence of implicit and explicit retrievals on the successful retrieval effect. Experiment 1 demonstrated significant vPPC activity for the old compared to the new words during an explicit Recognition task and an implicit LD task. We did observe greater activation in medial prefrontal regions during the explicit compared to the implicit retrieval, which is consistent with the previous studies (Fleck et al., 2006) and may reflect top-

Table 6

Experiment 2 regions active during cross-task analysis for [HC-Old>New_Recognition]>[Old>New_CD] contrast.

Region	Hemisphere	X (mm)	Y (mm)	Z (mm)	Z-score
Superior frontal gyrus	L	-22	22	60	3.88
	L	-4	40	54	3.83
Frontal pole	L	-22	22	54	3.78
	L	-16	64	6	3.77
Lateral occipital cortex	L	-14	58	30	3.65
	L	-46	-62	48	4.01
	L	-12	58	34	3.64
Lateral occipital cortex	L	-36	-56	40	3.36
	L	-56	-54	44	3.28
Angular gyrus	L	-42	-62	28	3.52
	L	-40	-70	40	3.28
Middle temporal gyrus	L	-38	-70	50	3.27
	L	-62	-42	-8	3.91
	L	-66	-48	-12	3.76
	L	-64	-44	-12	3.72
	L	-54	-46	-10	3.63
Posterior cingulate	L	-68	-28	-12	3.52
	L	-58	-32	-12	3.44
	L	-4	-40	38	4.15
Precuneous cortex	L	-12	-48	30	3.24
	L	-4	-48	34	3.21
	L	-2	-46	42	3.06
Inferior temporal gyrus	L	-2	-48	38	2.98
	L	-56	0	-34	3.23
	L	-50	0	-36	3.08
Middle temporal gyrus	L	-14	-50	34	2.9
	L	-60	-20	-32	3.3
	L	-58	-12	-32	3.1
	L	-60	-16	-32	3.07
	L	-58	-6	-32	3.03

down monitoring or post-retrieval processes that facilitate decision-making.

In the cross-task analyses, the vPPC old–new contrast was comparable between the explicit Recognition and implicit LD tasks. Although this difference was of similar magnitudes, both old and new items evoked greater activation in Recognition than the corresponding conditions in the LD task. It could be argued that unintentional explicit retrieval mediated successful retrieval effects during the LD task. However, this interpretation cannot account for the finding of the increased vPPC activity for new words during the explicit retrieval compared to the implicit retrieval, as novel items should not be accompanied by an episodic retrieval signal. An alternative interpretation is that the vPPC activation is an index of

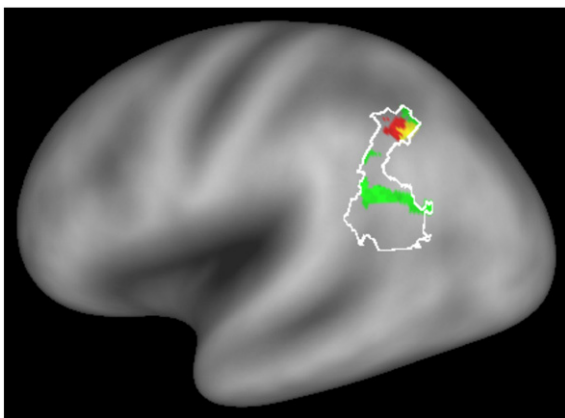


Fig. 4. Experiment 2 cross-task analysis. [HC-Old>New_Recognition]>[Old>New_CD] contrast in green and [Old>New_LD]>[Old>New_CD] contrast in red. The areas of overlap are in yellow. Threshold at $P < .05$, corrected.

how relevant the processing mnemonic status is to completing the task. Whereas old words may facilitate correct response for both tasks, new words are only particularly relevant in the Recognition task. That is, during the LD task all studied items were words while unstudied items carried no additional task-relevant information if the goal is merely to distinguish between words or non-words. Recognition performance depends on both identifying studied items as old *and* correctly rejecting unstudied items as new. This interpretation is consistent with our finding that old items evoked vPPC activity in both tasks, although to a greater extent during explicit Recognition as the task of judging mnemonic status was the primary objective. Likewise, the mnemonic status of the new items provided task relevant information in the Recognition but not LD task. The lack of differences in the magnitude of the successful retrieval effect may be explained by the fact that the different levels of activity for the new items between the tasks created a different “baseline” to which old items were compared. Although there was a greater activity for the old items in Recognition, the similarly elevated levels of activity in response to the new items prevented the old vs. the new contrast from being significantly greater than that found in the LD task.

Experiment 2 provided evidence that the successful retrieval effect is modulated by task relevance. While it has been shown that words are automatically processed to a certain extent (e.g. Stroop task), processing mnemonic status of each item is task irrelevant during the CD task as this feature provides no additional information towards facilitating a correct response. In the cross-task analyses, we replicated the finding of comparable differences between the old and new items in the Recognition and LD tasks. However, the difference between the old and new items during the CD task was substantially reduced. This finding argues against the role of unintentional explicit memory as driving the successful retrieval effect during the implicit LD task, because we would have expected the same unintentional processes to occur during the CD task. Instead, significant differences between the old and new items were only observed when stimulus activations arising from mnemonic status were relevant to task demands, and importantly, these differences occurred in similar locations when comparing both Recognition and LD tasks to the CD task.

A few issues should be addressed regarding differences across tasks. Reaction times tended to be longer during the Recognition task than either the LD or CD tasks. It is possible that a greater task difficulty (as measured by reaction time) may have contributed to a higher overall activation in the Recognition task. However, this would lead us to then expect greater activation for the new items which were associated with longer reaction times than the old items in both Recognition and LD, a result we did not find in either experiment. Also, our main findings were drawn from comparing within-task contrasts, which should help diminish effects present across task blocks unrelated to the differences in processing old vs. new items. An additional possibility is that the activity in the vPPC was gated by processing lexical rather than mnemonic features of the stimuli. If one assumes that subjects perform greater levels of lexical processing during the Recognition task than the CD task, this may be the case. While lexical processing may provide a binary gating of the vPPC activation, it does not appear to drive the magnitude of effects as the activation levels were highest in Recognition, not the LD task which required the greatest amount of lexical processing. Furthermore, similar levels of lexical processing are needed during the LD task for both the old and new items, yet we see both behavioral and BOLD response differences between these conditions. Overall, whether or not determining mnemonic status provides useful information towards completing the task goal remains a likely explanation for the pattern of results found here.

The present findings sharpen the conditions under which successful retrieval effects are observed. Implicit tasks may drive retrieval-related vPPC activity, but only if the task demands substantially

benefit from the detection of stored episodic features or relative novelty. With respect to the extant models, our findings may be interpreted as being consistent with an attentional account such as the AtoM model, as the vPPC activity is thought to index bottom-up sensory or hippocampally driven signals. The vPPC has been implicated in a gated form of stimulus-driven attention, such that only relevant stimuli produce bottom-up attentional capture (Indovina and Macaluso, 2007). In this case, the vPPC activity seen in our results may represent a target detection response to the MTL outputs (of both recollection and novelty signals) that are relevant to the current task. However, it should be noted that these bottom-up activations during attention tend to be right lateralized and located more anteriorly in the supramarginal gyrus than the more posterior and strongly left lateralized recollection-related activations. This raises the possibility that while target detection may occur in response to the mnemonic status, it is not the source of the successful retrieval effect. Our results also do not rule out alternative models such as the episodic buffer hypothesis. It is possible that the vPPC is serving as a passive store of information, however it does seem that this transfer from MTL to vPPC must pass through a filter. vPPC activation may also represent a process other than attention to or storage of retrieved information that facilitates memory retrieval, such as the cortical binding of episodic features (Shimamura, *in press*). In any event, the current study provides evidence that any such process is gated by task relevance.

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