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Neural correlates of metacognitive monitoring during episodic and semantic retrieval

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Abstract Activity in the posterior parietal cortex (PPC) has been shown to be a strong correlate of successful recognition performance. We assessed the degree to which the PPC mediates metacognitive judgments by assessing the feeling of knowing (FOK) for recently learned (episodic) and well-learned (semantic) facts (e.g., "The sport that is associated with Wimbledon is . . ."). Activity in ventral regions of the PPC was observed for strong FOKs for both sets of facts, although greater activity was observed for episodic than for semantic facts. Strong semantic FOKs activated anterior temporal regions. Weaker FOK ratings, when contrasted with strong FOKs, activated dorsal parietal regions, a finding that parallels contrasts during explicit tests in which low-confident responses were compared with high-confident responses. These findings demonstrate retrieval-related parietal activity during metacognitive judgments. Furthermore, they show that the ventral PPC is particularly engaged during context-specific, episodic retrieval, as compared to semantic retrieval.

Keywords Episodic memory · Semantic memory · Metacognition · Posterior parietal cortex

Metacognition refers to our ability to oversee or monitor cognitive processes (Metcalfe & Shimamura, 1994; Nelson & Narens, 1994; Shimamura, 2008). With respect to memory retrieval, behavioral studies have identified two metacognitive processes—trace access and inferential processes (Allen-Burge & Storandt, 2000; Koriat & Helstrup, 2007; Nelson, Gerler, & Narens, 1984). *Trace access* refers to retrieval of the actual features (i.e., traces) of a memory, some of which may only be partially retrieved, such as knowing that the name of Dorothy's dog in *The Wizard of Oz* begins with the letter "t" or has two syllables. Findings of positive correlations between feeling-of-knowing (FOK) ratings and subsequent recognition performance demonstrate the validity of trace-access processes (for a review, see Dunlosky & Bjork, 2008). *Inferential processes* do not directly tap traces, but instead depend on judging the probability of retrieval on the basis of general knowledge or the familiarity of the cue. For an inferential FOK, you might judge that you would likely recognize the name of Dorothy's dog, because you remember having watched the movie and think that you could recognize the dog's name. Behavioral findings have demonstrated that FOK judgments can be driven solely by inferential processes, such as cue familiarity (Metcalfe, Schwartz, & Joaquim, 1993).

Typically, FOK judgments are based only on items that cannot be fully retrieved. Thus, if you could overtly recall the name of Dorothy's dog as "Toto," that item would be discarded from the FOK analysis. As a result, extant studies tend to be biased toward inferential processes, because items with very strong (i.e., recallable) traces are removed from further analysis. Neurocognitive findings are consistent with the role of inferential processes for typical FOK judgments, as the prefrontal regions that are active during valid FOKs are also active in tasks that involve top-down executive control. Prefrontal activations have been observed for FOK judgments about general fact knowledge (Kikyo, Ohki, & Miyashita, 2002; Maril, Simons, Weaver, & Schacter, 2005) and about recently learned information (Schnyer, Nicholls,

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& Verfaellie, 2005; Schnyer et al., 2004). In the present study, we assessed all items, in order to evaluate neural responses to items with full trace access (i.e., those judged to be extremely high in FOK). Thus, our FOK analysis is unique, in that it includes items not usually assessed. However, metacognitive judgments do not necessarily have to assess only weak or nonrecallable information. Judgments of learning (JOLs), which are assessed soon after encoding, are based on all items learned, including those that are recallable (Nelson & Dunlosky, 1991).

To assess the neural correlates of FOKs more generally, we included items that are potentially recallable. To the extent that very strong FOKs are based largely on the successful retrieval of memory traces, our FOK findings can be linked to those from studies of overt memory performance. In such studies, the posterior parietal cortex (PPC) is particularly active, as evidenced on tests of old/new recognition memory when remembered items (hits) are compared with new items (correct rejections) (for reviews, see Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Shimamura, 2011; Vilberg & Rugg, 2008; Wagner, Shannon, Kahn, & Buckner, 2005). Moreover, ventral regions (vPPC, particularly the angular gyrus and posterior parts of the temporo-parietal junction) are associated with high-confident hits, whereas dorsal regions (dPPC, including the superior parietal lobule and the medial wall of the intraparietal sulcus) are associated with low-confident hits (Kim & Cabeza, 2009; Wheeler & Buckner, 2004). Low-confident hits also recruit prefrontal regions, suggesting that these areas, along with the dPPC, are involved when extensive executive (i.e., inferential) processes are required.

The neural correlates of successful retrieval have been assessed primarily on explicit memory tests, such as old/new recognition, source memory, and remember/know judgments (Kim & Cabeza, 2009; Vilberg & Rugg, 2007; Wheeler & Buckner, 2004). Analyses have shown that PPC activity also occurs for false recognitions and implicit retrieval, though not as strongly as for items remembered on explicit tests (Elman & Shimamura, 2011; Kahn, Davachi, & Wagner, 2004; Wheeler & Buckner, 2003). These findings are based on memory for recently learned material, such as words, faces, or pictures. Less is known about the successful retrieval of conceptual (semantic) information, such as memory for facts or general knowledge. Findings of greater vPPC activity for items associated with strong source memory or recollective responses suggest that this region may be preferentially engaged during retrieval of contextually based or episodic information (Daselaar, Fleck, & Cabeza, 2006; Dobbins, Foley, Schacter, & Wagner, 2002; Wheeler & Buckner, 2004; Yonelinas, Otten, Shaw, & Rugg, 2005).

In the present study, we addressed two questions: (1) Is PPC activity present during metacognitive (i.e., FOK) judgments, or is it restricted to tasks of explicit recognition tests? (2) Does PPC activity monitor retrieval of overlearned (semantic) information, as well as that of recently learned and contextually bound (episodic) information? To equate the task demands across conditions, we assessed memory for factual information (e.g., "The park in which Old Faithful is located is . . ."). For half of these items, FOKs were based on knowledge acquired prior to the experimental session and presumed to have been experienced on multiple occasions (i.e., semantic memory). The other facts were previously unfamiliar but were presented to the subjects just prior to scanning. Thus, for these recently learned facts, accurate FOKs would be based on retrieval of a specific episodic context. To our knowledge, this study represents the first to consider unrestricted FOK responses (i.e., those including potentially recallable items). Moreover, few studies have compared semantically and episodically based FOKs in the same study. Our central aim concerns the neural underpinnings of very strong FOKs, which are presumed to be largely based on accessing the memory traces of contextual features or conceptual familiarity. By evaluating the neural correlates of such responses—for both semantic and episodic information—we consider the degree to which PPC activity reflects monitoring of and operations on different types of retrieved information.

Method

Subjects

A group of 19 healthy subjects participated in this study (7 female, 12 male; mean age = 21.11 years, range = 18–33 years). Two additional subjects were excluded from the analysis due to excessive head motion and scanner artifacts. All subjects were paid for their participation and gave informed consent according to guidelines approved by the UC Berkeley Office for the Protection of Human Subjects. All of the subjects were native English speakers and right-handed, and none reported a history of neuropsychiatric disorders or brain injury or having recently taken psychoactive medication.

Stimuli

We used a set of 160 fact questions presented in the form of an incomplete sentence (e.g., "The sport that is associated with Wimbledon is . . ." [Answer: "tennis"]). Of these facts, 80 were common and generally well-known facts (henceforth identified as *semantic* facts), such as the Wimbledon question, whereas 80 other facts were more obscure (e.g., "The name of the number-two wood golf club is . . ." [Answer: "brassie"]). The answers to these obscure facts (henceforth identified as *episodic* facts), were presented to the subjects prior to scanning. Pilot tests showed that recall performance for the semantic facts was comparable to recall performance for the episodic facts after their answers had been presented. The word length of the fact sentences ranged from 7 to 24 words (mean = 13.94 words).

Behavioral procedure

Prior to scanning, the subjects were presented the answers to the episodic facts. On each study trial, a fact question was presented until a subject-paced buttonpress revealed the correct answer on screen for 3 s. The presentation order of the 80 episodic facts was randomized, and the study set was repeated for a second presentation. During the initial presentation of these facts, subjects identified any that they had known previously, and those items were excluded from the analysis (mean number of episodic facts excluded = 1.77).

In the scanner, approximately 30 min after the study session, the subjects were presented with four blocks of trials in which FOK judgments were requested. Each trial consisted of a fact question presented in the form of an incomplete sentence (4,000 ms), during the presentation of which the subjects rated how likely they would be able to recognize the correct answer in a multiple-choice test, followed by a central fixation cross (2,200–3,600 ms jittered). The response options were "definitely," "likely," "maybe," and "guess," which were made using thumb keypresses of each hand on a four-button response box. The response mappings were counterbalanced across subjects. Each block consisted of 40 FOK trials of either episodic or semantic facts. The order of presentation (semantic or episodic blocks) alternated, and this order was counterbalanced across subjects.

After scanning, the subjects were given a six-alternative forced choice recognition test for all 180 facts. The facts were presented in a random order, with each trial consisting of the incomplete sentence with six answer choices. The recognition test was self-paced, and subjects responded with a keypress corresponding to one of the six choices. To verify the FOK accuracy, we assessed recognition responses (correct vs. incorrect) as a function of FOK rating.

fMRI acquisition

The subjects were scanned in a 3 T Siemens (Erlangen, Germany) Trio scanner at the UC Berkeley Brain Imaging Center. For each of the four functional runs, we used a T2*-weighted echo-planar imaging (EPI) sequence (TR = 2,200 ms, TE = 26 ms, flip angle = 80 º, matrix = 100 × 100, FOV = 210 mm, 3-mm slice thickness) with GRAPPA (acceleration factor 2). Thirty-five axial slices oriented to the AC–PC line were acquired in a sequential descending order giving whole-brain coverage. A total of 118 volumes were collected during each of the functional-imaging runs. The first nine volumes of each run were discarded to allow for magnetization preparation. A high-resolution magnetization-prepared rapid-acquisition gradient echo (TR = 2,300 ms, TE = 2.98, matrix = 256 × 256, FOV = 256, sagittal plane, slice thickness = 1 mm, 160 slices) and a gradient-echo multislice (TR = 250 ms, TE = 22, matrix = 256 × 256, FOV = 256, 3-mm slice thickness, 37 slices) were collected for registration purposes.

fMRI data analysis

The data were preprocessed and analyzed with the FSL Toolbox, version 4.1.4 (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) sync 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 to separate brain from the surrounding skull and tissue in each volume. All images were spatially smoothed with a 5-mm full-width-at-half-maximum Gaussian kernel to reduce noise and allow for group analysis. High-pass temporal filtering was performed using the local Gaussian-weighted fit of a running line to remove low-frequency artifacts. The individual-subject data were 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, the 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 multilevel, mixed-effects general linear model was run using FILM (FMRIB's Improved Linear Model), which treated subjects as random effects. Individual runs from the FOK phase 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 double-gamma hemodynamic response function and the temporal derivative. Each correct response type was modeled separately for both conditions. Motion parameters were included as additional confound variables, and temporal autocorrelation was removed through prewhitening. Trials with no response and those corresponding to questions answered incorrectly at follow-up testing were also modeled as regressors of no interest. Contrasts were entered to compare levels of FOK and fact type (episodic vs. semantic).

A second-level analysis combined the runs for each subject using a one-sample *t* test, treating runs as fixed effects. Third-level group statistical 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 a slower Markov chain Monte Carlo–based analysis for all voxels identified as being near threshold in the first stage. The whole-brain family-wise error was corrected to $p < .05$ using Gaussian random field theory with a cluster-forming threshold of $z > 2.3$. Thresholded group maps were projected on to inflated atlases for display purposes using the CARET software (http://sumsdb.wustl.edu/sums/humanpalsmore.do; Van Essen, 2005).

Results

Behavioral results

Overall recognition performance was high, and somewhat better for episodic facts (92.5 % correct) than for semantic facts (88.8 % correct), $t(18) = 2.42$, $p < .05$. Response latencies were also significantly faster for episodic ratings (2,140.26 ms) than for semantic ratings (2,369.50 ms), $t(18) = -4.62$, $p < .001$ (see Table 1). The subjects, however, gave more "definitely" FOK ratings to semantic facts (69.1 %) than to episodic facts (53.9 %), $t(18) = -3.62$, $p < .01$. Table 2 displays the proportions of FOK responses elicited across the four rating categories ("definitely," "likely," "maybe," and "guess") and recognition performance within each category. The FOK ratings were valid, as recognition performance increased with FOK strength, $F(3, 138) = 17.21$, $p < .001$.

fMRI results

Feeling of knowing We grouped "likely" and "maybe" FOK ratings, in order to increase statistical power, and compared this combined set with the "definitely" FOK ratings. "Likely/maybe" responses reflect the kind of subthreshold or nonrecallable information typically assessed in FOK studies. Items rated as "definitely" recognizable, on the other hand, represent strong-FOK responses that have not been evaluated in previous studies, because many of these items would have been recallable and thus removed from the analysis. We first considered "definitely" > "likely/maybe" contrasts in order to reflect the activations underlying very strong FOK responses. The reverse, "likely/maybe" > "definitely" contrasts were also assessed, as they represent the neural processes engaged when weaker traces are evaluated, and they are presumed to depend more on top-down inferential processes. The latter contrast is similar to previous analyses of low- > high-confidence ratings assessed during recognition judgments (Kim & Cabeza, 2009; Wheeler & Buckner, 2004). "Guess" ratings were rarely elicited and are not evaluated in the following fMRI analyses.

Table 2 Proportions of feeling-of-knowing (FOK) responses by FOK strength, along with overall correct-response rates (in parentheses), for episodic and semantic facts

	Definitely	Likely	Maybe	Guess
Episodic	.54 (98 %)	.17 (94 %)	.18 (86 %)	.11 (74 %)
Semantic	.69 (95 %)	.13 (85 %)	.10 (74 %)	.08 (58 %)
TOTAL	.62 (97 %)	.15 (90 %)	.14 (82 %)	.09 (67 %)

These FOK strength categories refer to responses given by subjects during the scanned FOK phase, and accuracy is derived from performance during the subsequent recognition phase

Figure 1 shows the regional activations associated with contrasts of "definitely" > "likely/maybe" FOKs, assessed separately for episodic and semantic facts. This and the subsequent analyses only included correctly recognized facts. For both episodic and semantic facts, "definitely" FOK responses activated a broad set of cortical regions (see Table 3). In particular, there were large overlapping activations in the vPPC, medial parietal cortex (mPC), and mPFC. Within the parietal cortex, lateral activations were clustered in the angular gyrus and temporo-parietal junction. Medial parietal activations were clustered in the precuneus and posterior cingulate gyrus. Within the PFC, we found significant activations in ventrolateral (vLPFC) and dorsolateral regions. These regions, evoked by strong-FOK responses, are comparable to the regions activated in explicit-memory tests when information is successfully retrieved.

Weak-FOK responses ("likely/maybe" > "definitely") activated a less broad set of regions (see Fig. 2 and Table 4). For

Table 1 Reaction times by feeling-of-knowing (FOK) strength category are listed, with standard errors in parentheses

	Definitely	Likely	Maybe	Guess
Episodic	1,946 ms (64)	2,577 ms (150)	2,580 ms (91)	2,555 ms (87)
Semantic	2,341 ms (49)	2,887 ms (71)	2,862 ms (169)	2,715 ms (76)
TOTAL	2,168 ms (51)	2,710 ms (94)	2,682 ms (78)	2,624 ms (46)

These refer to responses given by subjects during the scanned FOK phase

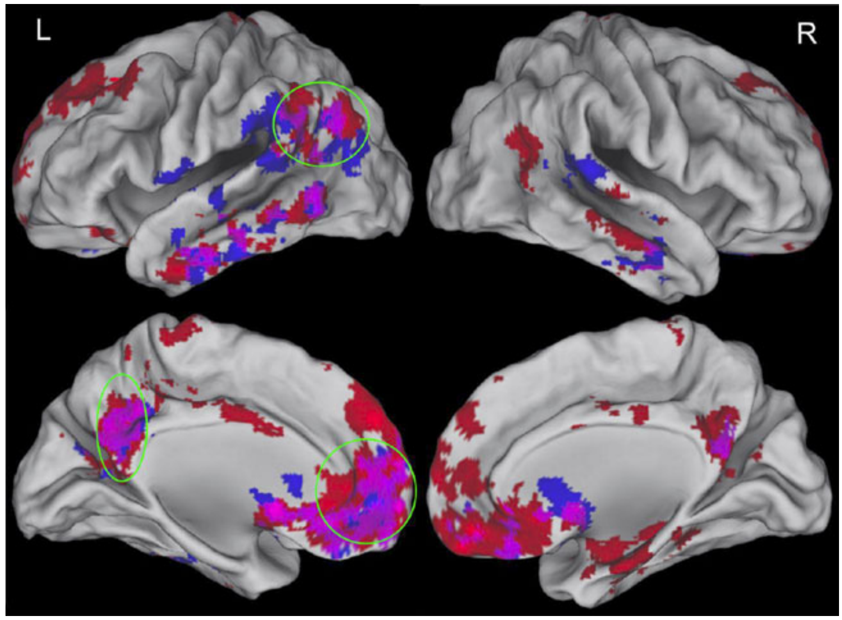

Fig. 1 Regional activity associated with strong-FOK ratings ("definitely" > "likely/maybe") for episodic (red) and semantic (blue) facts that were correctly recognized. Shown in purple are regions of overlap, which included the left vPPC, mPC, and mPFC (circled regions). Activations are projected onto lateral (top) and medial (bottom) views of an inflated atlas using the CARET software (Van Essen, 2005)

both episodic and semantic facts, significant activations were observed in bilateral dPPC, anterior cingulate gyrus, and right vLPFC. The dPPC and PFC activations are comparable to the activations observed on explicit tests when low-confident recognition hits are compared with high-confident hits. For episodic FOKs, weak responses were also associated with activations in the lateral occipital cortex (bilaterally) and left medial occipital cortex. Weak semantic FOKs were associated with activations in the inferior frontal gyrus.

Episodic versus semantic FOKs Differences in the patterns of activation between strong episodic and semantic FOK responses were assessed by contrasting "definitely" FOK ratings between the two sets. Figure 3 shows regional activations for the contrasts of episodic > semantic "definitely" FOKs (in red) and semantic > episodic "definitely" FOKs (in blue) (see also Table 5). Relative to semantic FOKs, strong episodic FOKs evoked greater activations in the left vPPC, precuneus, and frontal pole. These regions have been associated with high-confident hits during explicit retrieval (Kim & Cabeza, 2009). Relative to episodic FOKs, strong semantic FOKs activated the right anterior temporal lobe, a finding consistent with previous analyses of semantic processing (Martin & Chao, 2001; Mummery et al., 2000).

One possible concern of these analyses is the small but significant difference in the behavioral performance between the episodic and semantic conditions. Specifically, greater proportions of "definitely" FOK responses were elicited for semantic than for episodic facts, although overall recognition performance for the episodic facts was actually greater. Moreover, response latencies were faster for episodic FOK ratings than for semantic ratings. While prior work has shown that the vPPC is not modulated by the proportions of old and new items (Vilberg & Rugg, 2009), we examined the degree to which neural responses were driven by the proportion of "definitely" responses elicited across subjects. We generated an 8-mm spherical region of interest (ROI) centered on the voxel with the local maximum z score resulting from the contrast of "definitely" > "likely/maybe" ratings (MNI coordinates: $x = -38$, $y = -56$, $z = 34$) and extracted parameter estimates of "definitely" trials for each subject. We then correlated these values with each subject's proportion of "definitely" FOK responses. The correlations were not significant for either episodic ($r = -.24$, $p = .43$) or semantic ($r = -.23$, $p = .35$) facts.

We also evaluated the possibility that brain activity was driven by differences in response latencies between episodic and semantic FOKs. This factor was not likely to impact significantly on our results, for several reasons. First, the temporal derivative for each regressor allowed the model to flexibly fit the onset times by up to 1 s, a time greater than the difference found in the response latencies. Second, longer reaction times tend to evoke greater amounts of activity, yet we observed greater vPPC activity for items with faster response latencies (episodic FOKs). To address this issue directly, we extracted the percentage of signal change from the vPPC ROI described above and generated peristimulus plots separately for strong episodic and semantic FOKs. These values were compared to the mean activity of this

Table 3 Peak activations of significant clusters from the contrast of "definitely" > "likely/maybe"

Region	Hemisphere	*X* (mm)	*Y* (mm)	*Z* (mm)	*z* Score
Episodic "Definitely" > "Likely/Maybe" Contrast					
Angular gyrus	L	−46	−50	24	3.68
	R	48	−54	18	3.88
Frontal medial cortex	R	8	50	−14	4.55
Frontal orbital cortex	L	−28	34	−20	3.87
Frontal pole	R	6	54	−20	4.48
Inferior temporal gyrus	L	−62	−36	−22	3.62
	R	50	−10	−26	3.78
Lateral occipital cortex	L	−56	−66	−4	4.2
	R	54	−68	26	3.7
Middle frontal gyrus	L	−32	32	46	4.61
Middle temporal gyrus	L	−68	−42	−12	3.83
	R	62	−12	−10	3.64
Paracingulate gyrus	R	4	52	2	4.62
Parahippocampal gyrus	R	24	−20	−20	3.62
Postcentral gyrus	R	2	−36	66	3.68
Posterior cingulate	R	4	−52	28	3.88
Precuneous cortex	L	−10	−58	24	4.16
Subcallosal cortex	L	−2	8	−6	4.38
Temporal fusiform cortex	R	30	−36	−16	3.66
Semantic "Definitely" > "Likely/Maybe" Contrast					
Angular gyrus	L	−60	−54	34	3.64
Central opercular cortex	L	−56	−12	10	3.6
Frontal medial cortex	L	−2	42	−14	4.18
Inferior temporal gyrus	R	50	−10	−26	3.16
Lateral occipital cortex	L	−54	−62	−6	3.71
Middle temporal gyrus	L	−56	−62	−2	3.75
	R	58	0	−18	3.31
Paracingulate gyrus	L	−10	54	−4	4.23
Posterior cingulate	L	−4	−50	26	3.31
Precuneus cortex	L	−4	−66	20	3.54
Subcallosal cortex	L	0	8	−6	3.64
Superior temporal gyrus	R	62	−34	10	3.94
Supramarginal gyrus	R	56	−38	8	3.45
Caudate	R	10	18	2	3.58
Parietal operculum cortex	L	−52	−38	24	4.02
Planum temporale	R	58	−26	10	3.4

The results are separated by condition (episodic or semantic)

ROI over the entire course of each run. The onset and the temporal pattern of activation were similar across conditions, with the only difference being the magnitude of the response (see Supplementary Fig. 1). Thus, the temporal dynamics of the BOLD signal across conditions within the vPPC did not appear to be influenced by the rather small difference in response latencies. This does not rule out the possibility that regions outside of the vPPC displaying significant activity were modulated by reaction time, and in fact, such modulations are quite likely in regions such as the PFC (Henson, Rugg, Shallice, & Dolan, 2000).

Discussion

Previous FOK studies have focused primarily on the PFC's role in mediating FOK judgments (Janowsky, Shimamura, & Squire, 1989; Kikyo et al., 2002; Maril et al., 2005; Maril,

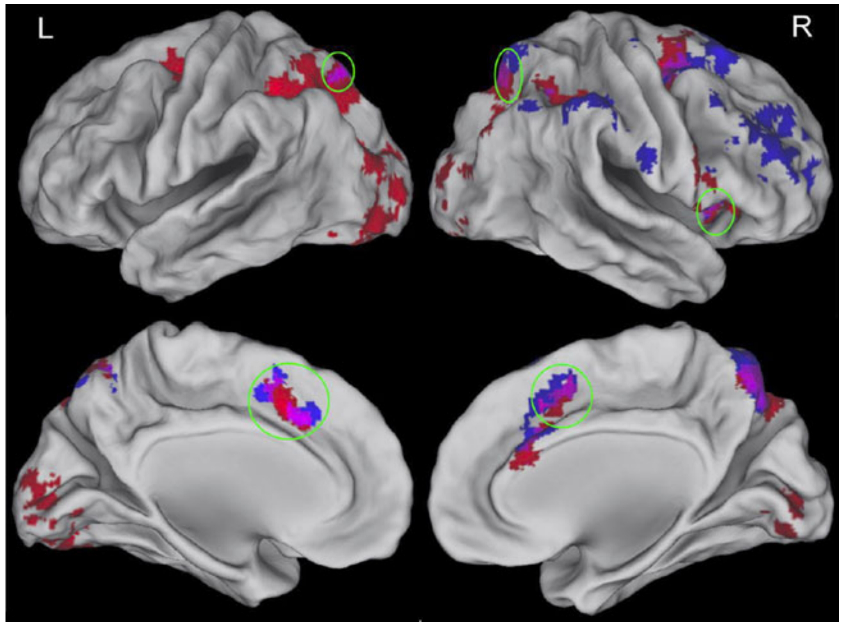

Fig. 2 Regional activity associated with weak-FOK responses (“likely/maybe” > “definitely”) for episodic (red) and semantic (blue) facts that were correctly recognized. Shown in purple are regions of overlap, which included bilateral dPPC, anterior cingulate, and right vLPFC (circled regions). Activations are projected onto lateral (top) and medial (bottom) views of an inflated atlas using the CARET software (Van Essen, 2005)

Wagner, & Schacter, 2001; Reggev, Zuckerman, & Maril, 2011; Schnyer et al., 2005). As mentioned above, these prior studies restricted analyses to FOK ratings of nonrecalled information. Thus, the prior studies did not consider the neural underpinnings of very strong FOK responses. The present study assessed the neural correlates of episodic and semantic facts judged as “definitely” recognizable. Such strong-FOK responses activated a broad neural circuit that included vPPC, mPC, and mPFC (see Fig. 1). These same regions have been associated with recollection-related activations during explicit-memory tests (see Cabeza et al., 2008; Shimamura, 2011; Vilberg & Rugg, 2008). Furthermore, we were able to directly compare metacognitive monitoring of recently learned (episodic) and well-learned (semantic) information using the same kinds of test materials (i.e., general information facts). Strong episodic FOKs specifically activated vPPC, mPC, and anterior PFC, whereas strong semantic FOKs activated the right anterior temporal gyrus (see Fig. 3).

The inclusion of potentially recallable information allowed us to examine more directly the contribution of trace-access processes and to link these findings to studies of explicit retrieval. Strong FOKs elicited activations similar to those observed during successful recognition (hits > correct rejections) and demonstrated the contribution of the vPPC during metacognitive monitoring. Thus, even in such metacognitive analysis, in which individuals are assessing their confidence of retrieving information, the vPPC is active. The role of the vPPC in mediating confidence judgments is consistent with studies of patients with parietal lesions (Davidson et al., 2008; Simons, Peers, Mazuz, Berryhill, & Olson, 2010). Although patients with parietal lesions do not exhibit significant impairment in recognition performance or source memory, they elicit fewer high-confident recognition responses or responses based on recollection as opposed to familiarity.

Whereas the vPPC was active during strong FOK judgments, the dPPC was active during weak FOK judgments (“likely/maybe” > “definitely”). In two previous studies (Maril et al., 2005; Reggev et al., 2011), PPC activity was observed when subjects assigned FOK ratings for nonrecallable facts rather than “don’t know” responses. We suggest that such PPC activity can now be distinguished between vPPC activations, driven by trace access, and dPPC activations, driven by inferential processes. This ventral–dorsal dissociation has also been observed in comparisons of high- versus low-confidence ratings that follow recognition judgments (Kim & Cabeza, 2009; Wheeler & Buckner, 2004). We suggest that the dPPC, along with PFC, is particularly involved when trace access is weak or not readily available. Under such conditions, greater involvement of top-down, inferential processes is necessary.

With respect to PFC processes, the posterior vLPFC was active for both episodic and semantic retrieval, particularly for weak-FOK responses. This region has been associated the selection and maintenance of information (Shimamura, 2008; Wagner, 2002). Also, right PFC activity for weak-FOK responses is consistent with conditions in which recollective processes fail and the monitoring of item familiarity becomes necessary (Dobbins, Simons, & Schacter, 2004; Henson et al., 2000). This same pattern was observed in the anterior cingulate gyrus for both episodic and semantic FOKs.

Table 4 Peak activations of significant clusters from the contrast of "likely/maybe" > "definitely"

Region	Hemisphere	*X* (mm)	*Y* (mm)	*Z* (mm)	*z* Score
Episodic "Likely/Maybe" > "Definitely" Contrast					
Anterior cingulate	R	8	28	20	4.58
Frontal operculum cortex	R	44	14	2	3.62
Frontal orbital cortex	R	32	26	−4	4.08
Insular cortex	R	30	16	8	3.4
Intracalcarine cortex	R	12	−82	2	3.55
Lateral occipital cortex	L	−18	−66	46	4.23
	R	18	−72	48	5.24
Lingual gyrus	L	−16	−88	−2	3.62
Occipital fusiform gyrus	R	26	−78	−8	3.43
Occipital pole	L	−34	−92	−18	3.87
Paracingulate gyrus	L	−6	14	40	3.69
	R	2	8	50	4.37
Precentral gyrus	L	−26	−10	54	4.11
	R	26	−12	48	3.59
Precuneus cortex	R	8	−66	50	3.79
Superior frontal gyrus	L	−22	−4	48	4.17
	R	22	−2	56	4.17
Superior parietal lobule	L	−34	−48	48	3.85
	R	30	−48	44	3.77
Supramarginal gyrus	R	42	−36	42	3.73
Semantic "Likely/Maybe" > "Definitely" Contrast					
Anterior cingulate	R	12	28	16	3.36
Frontal orbital cortex	R	36	22	−12	3.52
Frontal pole	R	36	46	32	3.86
Inferior frontal gyrus	R	52	14	−2	2.93
Insular cortex	R	32	18	6	3.12
Lateral occipital cortex	R	10	−76	52	4.76
Middle frontal gyrus	R	28	4	52	4.02
Paracingulate gyrus	L	−2	28	34	3.38
	R	2	16	44	4.5
Precuneus cortex	R	12	−66	48	4.26
Superior frontal gyrus	R	14	22	60	4.18
Supplementary motor cortex	R	4	6	50	4.5
Supramarginal gyrus	R	48	−38	44	4.13

The results are separated by condition (episodic or semantic)

It has been suggested that this region monitors response conflict and may signal a demand for further reflective processing (Raye, Johnson, Mitchell, Nolde, & D'Esposito, 2000). This heightened demand for postretrieval processing may further be reflected in the longer reaction times associated with weak-FOK trials. While PFC activation was largely domain general, there were some differences between the conditions. Specifically, the left frontal pole was more active during episodic FOKs, as compared to semantic FOKs. This region has been implicated in the monitoring of context-specific retrieval, which would be more critical for recently learned (episodic) facts (Dobbins et al., 2004; Rugg, Fletcher, Chua, & Dolan, 1999).

In the present study, the vPPC was associated with strong-FOK responses for both episodic and semantic facts, although there was significantly greater activation in this region for episodic facts. This finding is consistent with a recent theory of memory retrieval that suggests that the vPPC is involved in the cortical binding of relational activity (CoBRA) (Shimamura, 2011). According to CoBRA, the vPPC acts as a neocortical convergence zone that integrates or binds features associated with a past experience or event.

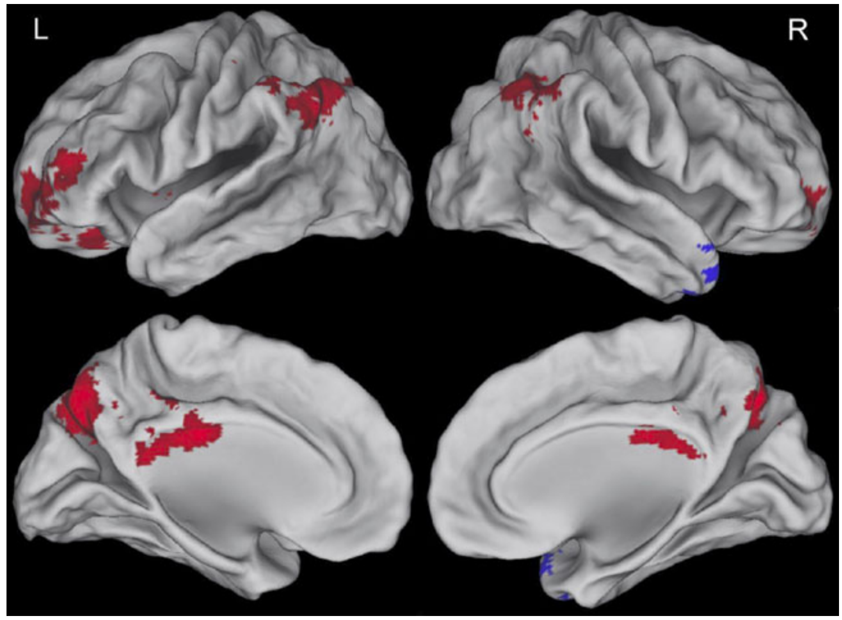

Fig. 3 Direct contrasts of strong ("definitely") FOKs for correctly recognized episodic and semantic facts. Shown in red are regions evoked specifically by strong episodic FOKs (episodic > semantic), which included bilateral vPPC, mPC, and left anterior PFC. Shown in blue are regions evoked specifically by strong semantic FOKs (semantic > episodic), which included the right anterior temporal gyrus. Activations are projected onto lateral (top) and medial (bottom) views of an inflated atlas using the CARET software (Van Essen, 2005)

At the time of encoding, the medial temporal cortex initially binds features of specific episodic events, as suggested by extant consolidation theories (see Eichenbaum, Otto, & Cohen, 1992; Shimamura, 2010; Squire & Alvarez, 1995). Through reminiscence or replay, neocortical links between episodic features are established, many of which depend on intermodal bindings within the vPPC. During retrieval, vPPC links contribute significantly to the reinstatement or "re-collection" of event features specific to a prior episode or experience. Episodic retrieval depends specifically on the recollection of event features. Retrieval of semantic knowledge or other information experienced on multiple occasions (e.g., faces of friends) may also depend on multimodal bindings, though not to the same extent as retrieving a specific event or experience. As this idea applies to our study, when subjects are presented a sentence stem previously encountered during the study session, the FOK decision is likely based on the strength of memory traces associated with the study session. That is, trials in which the cue is more tightly bound to the learning context give rise to stronger FOK responses. In contrast, FOK decisions during the semantic condition must be based on a more

Table 5 Peak activations of significant clusters from direct comparisons of the episodic versus semantic conditions

Region	Hemisphere	*X* (mm)	*Y* (mm)	*Z* (mm)	*z* Score
Episodic "Definitely" > Semantic "Definitely" Contrast					
Angular gyrus	L	−40	−50	38	4.47
	R	48	−56	52	4.24
Central opercular cortex	L	−46	−4	4	3.49
Frontal pole	L	−38	54	2	4.43
	R	26	60	−4	3.71
Heschl's gyrus	L	−44	−14	4	2.97
Insular cortex	L	−42	4	−2	3.45
Lateral occipital cortex	L	−42	−68	48	3.82
Posterior cingulate	L	0	−24	26	4.11
	R	4	−20	26	4.05
Precuneus cortex	L	−10	−78	42	4.58
	R	12	−68	42	4.32
Supramarginal gyrus	L	−44	−42	38	3.8
Semantic "Definitely" > Episodic "Definitely" Contrast					
Temporal pole	R	50	24	−22	3.9

Only "definitely" responses were included in order to equate feeling-of-knowing strength between conditions general familiarity with information relating to the fact. In a recent study (Elman, Cohn-Sheehy, & Shimamura, 2012), retrieval-related activity to spatial locations (i.e., photographs of buildings) learned during a recent study session was compared to retrieval of well-known spatial locations (i.e., familiar campus buildings). The vPPC was particularly active for recently learned spatial locations as compared to familiar ones, just as the present study showed significant vPPC activation for recently learned facts.

In summary, the present findings refine and extend the conditions under which the parietal cortex contributes to retrieval-related processes. When individuals have strong FOK experiences, vPPC regions are recruited, which are known to be involved during the explicit retrieval of episodic features or traces. Strong FOKs for well-learned semantic facts activated the anterior temporal cortex, a region associated with semantic knowledge networks. Weak-FOK responses to both episodic and semantic facts were associated with increased dPPC and PFC activity, a finding that suggested a domain-general network involved in top-down executive search strategies. Thus, the results of the present findings help define and distinguish PPC involvement during metacognitive monitoring of episodic and semantic memory.

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