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Goal-dependent modulation of declarative memory: Neural correlates of temporal recency decisions and novelty detection

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Abstract

Declarative memory allows an organism to discriminate between previously encountered and novel items, and to place past encounters in time. Numerous imaging studies have investigated the neural processes supporting item recognition, whereas few have examined retrieval of temporal information. In the present study, functional magnetic resonance imaging (fMRI) was conducted while subjects engaged in temporal recency and item novelty decisions. Subjects encountered three-alternative forced-choice retrieval trials, each consisting of two words from a preceding study phase and one novel word, and were instructed to either identify the novel item (Novelty trials) or the more recently presented study item (Recency trials). Relative to correct Novelty decisions, correct Recency decisions elicited greater activation in a network of left-lateralized regions, including frontopolar and dorsolateral prefrontal cortex and intraparietal sulcus. A conjunction analysis revealed that these left-lateralized regions overlapped with those previously observed to be engaged during source recollection versus novelty detection, suggesting that during Recency trials subjects attempted to recollect event details. Consistent with this interpretation, correct Recency decisions activated posterior hippocampus and parahippocampal cortex, whereas incorrect Recency decisions elicited greater anterior cingulate activation. The magnitude of this latter effect positively correlated with activation in right dorsolateral prefrontal cortex. Finally, correct Novelty decisions activated the anterior medial temporal lobe to a greater extent than did correct Recency decisions, suggesting that medial temporal novelty responses are not obligatory but rather can be modulated by the goal-directed allocation of attention. Collectively, these findings advance understanding of how subjects strategically engage frontal and parietal mechanisms in the service of attempting to remember the temporal order of events, and how retrieval goals impact novelty processing within the medial temporal lobe.

Keywords: Recognition memory; Episodic memory; Recollection; Familiarity; Temporal context; Retrieval orientation

1. Introduction

Declarative memory supports remembering *what* items have been encountered, as well as *when* they were experienced. Discrimination between experienced and novel items can be based on recollection—the retrieval of specific contextual details associated with the item's occurrence – or on familiarity – the sense of having encountered the item in the absence of any specific details (Yonelinas, 2002). Paralleling item recognition, it has been argued that recognizing *when* an item was experienced can be based on recollecting details about the temporal context in which the item appeared, or on an assessment of trace-strength or item familiarity (Curran & Friedman, 2003; Hintzman, 2001, 2003, 2005). Although considerable attention has been focused on specifying the neural mechanisms that support recollection- and familiarity-based item recognition (Aggleton & Brown, 1999; Curran, 2000; Duzel, Yonelinas, Mangun, Heinze, & Tulving, 1997; Eldridge, Knowlton, Furmanski, Bookheimer, & Engel, 2000; Gonsalves, Kahn, Curran, Norman, & Wagner, 2005; Norman & O'Reilly, 2003; Ranganath et al., 2004; Squire, Stark, & Clark, 2004; Wheeler & Buckner, 2004), relatively less is known about the neural processes supporting retrieval judgments about temporal information. Moreover, the few neuroimaging studies that have sought to delineate the processes supporting temporal recency decisions have yielded conflicting evidence as to whether such decisions depend on the recollection of event details or on assessments of item familiarity, with these differences potentially stemming from different task constraints across studies.

Specifying which prefrontal cortical (PFC) mechanisms are engaged during temporal recency decisions may provide

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leverage on understanding the bases for such judgments. Extensive prior neuroimaging evidence indicates that left lateral PFC regions – most notably frontopolar and dorsolateral cortices – are selectively engaged when subjects attempt to recollect contextual details about an episode, such as the spatial position in which a stimulus appeared (e.g., Cansino, Maquet, Dolan, & Rugg, 2002; Rugg, Fletcher, Chua, & Dolan, 1999) or perceptual or conceptual details associated with the item's prior encounter (e.g., Dobbins, Foley, Schacter, & Wagner, 2002; Dobbins & Wagner, 2005; Nolde, Johnson, & D'Esposito, 1998; Ranganath, Johnson, & D'Esposito, 2000). By contrast, right dorsolateral and ventrolateral PFC are often engaged when subjects attempt to make familiarity-based discriminations between novel and experienced items (Dobbins & Wagner, 2005; Henson, Shallice, & Dolan, 1999; Henson, Rugg, Shallice, & Dolan, 2000; Kensinger, Clarke, & Corkin, 2003). A central question with respect to understanding the bases of temporal recency judgments is: which PFC subregions are engaged during recency decisions relative to item recognition judgments?

Neuropsychological and electrophysiological studies have implicated PFC in temporal-order or temporal-recency decisions, though the specific PFC subregions associated with such judgments are unclear. Neuropsychological studies indicate that damage to lateral PFC impairs temporal-order retrieval to a greater extent than item recognition (Kesner, Hopkins, & Fineman, 1994; Milner, Corsi, & Leonard, 1991; Shimamura, Janowsky, & Squire, 1990); however, these effects often appear to be lateralized by stimulus type rather than type of retrieval decision. Electrophysiologically, while event-related brain potentials (ERPs) at bilateral PFC electrode sites have been observed to be more positive during correct recency retrieval compared with item recognition (Tendolkar & Rugg, 1998) and during contextually-driven recency decisions compared with those that were less driven by contextual retrieval (Curran & Friedman, 2003), it is difficult to discern the neural generators of these effects, and thus it is unclear which specific PFC subregions contribute to such recency decisions.

Initial results from positron emission tomography and fMRI studies, while offering higher spatial resolution than ERP and most patient studies, have yielded conflicting patterns. On the one hand, the results from a few studies suggest a preferential role of right PFC subregions during temporal recency retrieval compared to item recognition (Cabeza, Anderson, Houle, Mangels, & Nyberg, 2000; Cabeza et al., 1997) and to conceptual source recollection (Dobbins, Rice, Wagner, & Schacter, 2003). These studies used relatively long lists of study items (60–80 items/list), which may have increased the probability that performance on temporal Recency trials was differentially dependent on familiarity. By contrast, other studies suggest that temporal recency retrieval can recruit left PFC regions typically involved in attempts to recollect source or contextual information (Konishi et al., 2002; Suzuki et al., 2002). These latter studies used relatively short lists of study items (10–30 items/list) and manipulated the nature of recency decisions by comparing "high demand" Recency trials, in which test items had appeared close together in the original study list, with "low demand" Recency trials, in which test items had appeared farther apart at study (Konishi et al., 2002) or by comparing within-list recency decisions with between-list recency decisions (Suzuki et al., 2002). These latter studies suggest that the conditions that elicit activation in left PFC subregions are those that decrease subjects' ability to rely on marked differences in item familiarity as a basis for their recency judgments, thus demanding contextual recollection for accurate performance.

A complicating factor for understanding the relation between studies demonstrating increased left PFC activation during "demanding" recency conditions and those revealing right PFC activation during recency relative to item recognition judgments is the fact that a number of the studies in the latter group failed to match the nature of the test probes across conditions (Cabeza et al., 1997, 2000; Eyler Zorrilla, Aguirre, Zarahn, Cannon, & D'Esposito, 1996; Nyberg et al., 1996; Rajah & McIntosh, 2006; Suzuki et al., 2002). Specifically, the item memory test probes in these experiments contained novel items, whereas the temporal recency test probes consisted of studied items. Accordingly, the first objective of the current study was to investigate the pattern of PFC activation during temporal recency versus item recognition decisions, while ensuring that the test probes were matched across conditions. We further sought to directly compare the pattern of PFC activation during temporal recency decisions with that seen in prior studies of source recollection.

Beyond PFC, other data indicate that the medial temporal lobe (MTL) may differentially contribute to temporal recency and item recognition decisions. For example, rodent studies have suggested a distinct role of the hippocampus in encoding and retrieving the temporal order of a sequence of events (Fortin, Agster, & Eichenbaum, 2002; Kesner, Gilbert, & Barua, 2002). In humans, some studies of patients with MTL lesions have demonstrated that such damage can disproportionately impair temporal-order memory in comparison to item recognition (Downes, Mayes, MacDonald, & Hunkin, 2002; Kopelman, Stanhope, & Kingsley, 1997; Mayes et al., 2001), whereas other studies have demonstrated either relatively spared temporal recency memory despite chance-level item memory (Sagar, Gabrieli, Sullivan, & Corkin, 1990) or impairments in both temporal-order memory and item recognition (Hopkins, Kesner, & Goldstein, 1995).

Recent neuroimaging evidence suggests that the MTL is recruited as recency retrieval demands increase (Konishi et al., 2002), as well as when recency decisions involve items that were studied in a relational as opposed to item-based manner (Konishi, Asari, Jimura, Chikazoe, & Miyashita, 2006). By contrast, other studies have revealed increased MTL activation during item recognition in comparison with temporal recency retrieval (Cabeza et al., 1997, 2000), though in these instances the comparisons of recency and item recognition trials were confounded by the presence of a novel item solely on item recognition trials. Because the MTL is known to differentially respond to the presence of novel stimuli (e.g., Dolan & Fletcher, 1997; Habib, McIntosh, Wheeler, & Tulving, 2003; Kirchhoff, Wagner, Maril, & Stern, 2000; O'Kane, Insler, & Wagner, 2005; Stark & Squire, 2001; Tulving, Markowitsch, Craik, Habib, & Houle, 1996), one interpretation for these latter effects is that the enhanced MTL responses during item recognition may have

reflected differential novelty detection processes. Alternatively, it is possible that greater MTL activity during item recognition versus temporal recency judgments may reflect a goal-directed shift in attentional orienting, wherein there is greater orienting towards item novelty on item recognition trials but greater orienting towards recollected contextual details on Recency trials. From this latter perspective, a person's retrieval goal may influence the processes engaged during retrieval attempts by (a) modulating the nature of the information processed within, and perhaps emerging from, the MTL memory system, and/or (b) affecting post-retrieval processes brought to bear on such information. Accordingly, a second goal of the present study was to determine whether MTL responses to identical retrieval cues are modulated by the subject's retrieval goal, which would indicate that goal-directed shifts in attention can regulate processing within the MTL.

In the present event-related fMRI study, we investigated the neural processes underlying temporal recency and novelty detection judgments. Importantly, the retrieval cues were matched such that all test trials consisted of two studied items and one novel item, thus ensuring that the critical factor that varied between conditions was the subject's retrieval goal (to assess relative recency versus detect item novelty). Motivated by the existing literature, we predicted that, relative to novelty detection, temporal recency decisions would involve (a) greater attempts to recollect event details and, in the face of recollection failure, (b) increased monitoring of the relative trace strength or familiarity of studied items. Specifically, we expected that during temporal recency trials, we would observe activation in the same left PFC and parietal regions implicated in previous studies of source or context recollection (Dobbins et al., 2002, 2003; Dobbins & Wagner, 2005; Ranganath et al., 2000). By contrast, we hypothesized that familiarity monitoring would be differentially engaged when contextual recollection failed, and thus we expected that activation in right PFC subregions previously associated with the monitoring of familiarity (Henson et al., 1999, 2000) would be greater on incorrect versus correct Recency trials. Finally, when the retrieval goal requires novelty detection, we predicted increased MTL activation, suggesting that MTL novelty responses are not obligatory but rather are modulated by how attention is allocated in the service of satisfying mnemonic task demands. A companion behavioral experiment assessed whether such goal-directed shifts in attention to item novelty has a functional consequence—namely, enhanced item encoding.

2. Methods

2.1. Subjects

Eighteen right-handed, native English speakers (nine female; age range, 18–27 yrs, mean = 20.6 yrs) were paid US$ 40 for their participation in the fMRI experiment. Data from two additional subjects were excluded from analysis, one due to excessive motion and a second due to poor behavioral performance (accuracy on the novelty detection task was 7 standard deviations below the group mean). An additional 12 subjects were paid US$ 15 for participation in the companion behavioral study. For all subjects, informed consent was obtained consistent with the institutional review board at Stanford University.

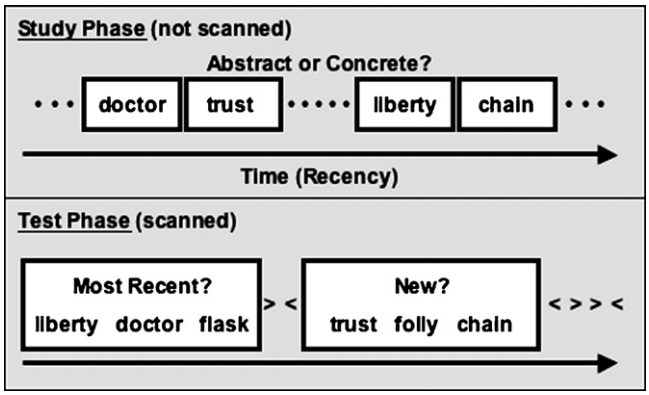

Fig. 1. The experimental design consisted of two main phases, study and test. During each unscanned study phase, participants made abstract/concrete judgments for each individual word. After a 30-s filled retention interval, participants were scanned while making Novelty and Recency decisions. On each trial, three words (two from the preceding study phase and one new) were presented; participants were asked to either select the novel word or the most recently presented study word.

2.2. Materials

The stimuli consisted of 396 nouns (198 abstract; 198 concrete). Abstract and concrete noun sets were matched for word length (range = 4–9 letters; mean = 6.5) and word frequency (range = 1–847; mean = 54.5). Of these words, 272 were divided into 8 lists of 34 study items. Each list was evenly split between abstract and concrete words, and the lists were matched on mean word length and word frequency. The remaining 124 words served as novel items in the test trials. Mean word length and word frequency for these novel items did not differ from that for studied items.

2.3. Procedure

The experiment consisted of eight cycles of the following three phases: study phase, retention interval, and test phase (Fig. 1). For all three phases, subjects made manual responses using a keypad under their right hand. Each cycle began with a (non-scanned) 136-s study phase, during which subjects made an abstract/concrete decision for each of the 34 words. Each word was presented for 2 s, with an inter-trial fixation interval of 2 s between stimuli. The study phase was followed by a (non-scanned) 30-s filled retention interval, consisting of 18 s of an *n*-back spatial working memory task using dot patterns followed by 12 s of fixation.

Subjects were scanned while engaging in the test phase, which consisted of three-alternative forced-choice trials (Fig. 1). All test trials shared an identical structure, and thus were matched for stimulus history and number of test probes per trial. Specifically, each trial consisted of two old words that had been encountered in the immediately preceding study phase and one new word. The location of old and new words across the three spatial positions (left, center, and right) was counterbalanced across trials. On Recency trials, subjects were cued to indicate the word that they had seen most recently ("Most Recent?"). On Novelty trials, subjects were cued to indicate the novel item ("New?"). The task cue appeared simultaneously with the test probes (Fig. 1). Each test phase contained 6 Novelty trials, resulting in a total of 48 Novelty trials across runs, and either 9 or 10 Recency trials, resulting in a total of 76 Recency trials across runs. The two old items within a test trial were selected such that they had appeared either 16 or 17 items apart during the study phase. Each trial was presented for 5 s followed by a 1-s fixation; subjects were instructed to make their responses during the 5 s that the test probes appeared on the screen. Test trials were intermixed in an event-related manner with variable duration null periods (2–6 s) consisting of 2-s trials of a simple arrows task, wherein subjects pressed one of two keys to indicate the direction (left or right) to which an arrow pointed (Stark & Squire, 2001). The order of study items and test trials were counterbalanced across subjects. Importantly, across subjects each studied item appeared in both Recency and Novelty test trials.

2.4. fMRI data acquisition

Whole-brain imaging was performed on a 3T Signa MRI system (GE Medical Systems). Prior to functional imaging, T2-weighted flow-compensated spin-echo anatomical images [repetition time (TR) = 3000 ms; echo time (TE) = 70 ms] were acquired from 24 contiguous 5-mm axial slices parallel to the AC–PC plane. Functional images, co-localized to the anatomical images, were acquired using a $T2^*$-weighted 2D gradient echo spiral-in/out pulse sequence [TR = 2000 ms; TE = 30 ms; 1 interleave; flip angle = 70°; FOV = 20 cm; 64 × 64 voxels] (Glover & Law, 2001). A total of 552 functional volumes were acquired for each subject across the eight functional scans. Four discarded volumes (a total of 8 s) were collected at the beginning of each scan to allow for T1 stabilization. A bite bar was used to minimize head motion.

2.5. fMRI data analysis

All imaging data were preprocessed using SPM2 (Wellcome Department of Cognitive Neurology, London). Functional images were corrected for differences in slice acquisition timing, followed by motion correction. Structural data were co-registered to the functional data and then segmented into gray and white matter and CSF. The gray matter was then stripped of any remaining skull and normalized to a gray matter MNI template image. Both structural and functional data were then normalized to this skull-stripped gray matter template. Images were resampled into 3-mm cubic voxels and spatially smoothed with an 8-mm FWHM isotropic Gaussian kernel.

The data were analyzed in SPM2 under the assumptions of the general linear model (GLM) with subjects treated as a random effect. Volumes were treated as a time series, and trials were modeled as 5-s epochs convolved with a canonical hemodynamic response function starting at the trial onset time without temporal derivatives. Correct and incorrect trials were modeled separately. The resulting functions were entered into a GLM, together with a basis set that served to high-pass filter the data and a covariate representing session effects. Linear contrasts were used to obtain subject-specific estimates for each effect. These estimates were entered into a second-level analysis treating subjects as a random effect, using a one-sample *t*-test against a contrast value of zero at each voxel. Unless stated otherwise, effects in a priori expected regions – in lateral PFC, parietal cortex, and MTL – were considered significant if they exceeded an uncorrected threshold of $p < .001$ and consisted of five or more contiguous voxels. With the exception of contrasts investigating retrieval success effects, all contrasts were performed using only correct trials.

Region of interest (ROI) analyses were used to supplement the voxel-based comparisons. ROIs included all significant voxels within a 6-mm radius of a targeted maximum. Deconvolution was performed using MarsBaR (http://marsbar.sourceforge.net), thus allowing assessment of the percent signal change associated with each condition.

3. Results

3.1. Behavioral results

In the fMRI experiment, accuracy differed between the two retrieval tasks ($t(17) = 17.00$, $p < .0005$), with participants performing more accurately on the Novelty task (.93) than on the Recency task (.65) (Table 1). Because performance on the Novelty task was near ceiling, chance performance on the Recency task was considered to be .50. Importantly, accuracy on the Recency task was above chance ($t(17) = 7.35$, $p < .0005$). Due to technical difficulties, reaction time data were not collected from two of the subjects. For the remaining 16 subjects, mean reaction times on correct trials differed between the two tasks ($t(15) = 6.77$, $p < .0005$), with participants taking longer on Recency than on Novelty trials (Table 1). Participants also took significantly longer on incorrect Recency trials than on correct Recency trials ($t(15) = 3.34$, $p < .005$).

Table 1
Behavioral performance for the recency and novelty tasks, as well as the number of trials falling into each condition

	Proportion	RT (ms)	No. of trials
Recency			
Correct	.65 (.09)	2906 (339)	49.7 (6.7)
Incorrect	.33 (.09)	3073 (442)	25.4 (6.8)
Novelty			
Correct	.93 (.05)	2343 (386)	44.7 (2.4)
Incorrect	.06 (.05)	3011 (810)	2.9 (2.4)

Scores are means. Standard deviations are in parentheses.

3.2. fMRI results

3.2.1. Neural correlates of temporal recency decisions

Our first objective was to delineate how the neural correlates of declarative remembering differ across temporal recency decisions relative to novelty detection. Comparison of correct Recency trials to correct Novelty trials revealed greater activation in a number of a priori expected lateral PFC and parietal regions, predominantly in the left hemisphere. Specifically, Recency trials elicited greater activation in left frontopolar cortex (FPC; ∼BA 10), left mid-dorsolateral PFC (∼BA 9/46), and left intraparietal sulcus (∼BA 7) (Fig. 2A; Table 2). An additional PFC response was observed in right superior frontal cortex (∼BAs 6/8) (Table 2), in a region falling close to that observed by Dobbins et al. (2003) to be differentially active during temporal recency decisions.

Because overall accuracy on the Recency task was relatively low (and was considerably lower than accuracy on the Novelty task), some of the correct Recency trials likely reflect guessing rather than memory retrieval. To ensure that the observed differences between Recency and Novelty trials reflect differences in memory retrieval, we performed a second analysis, this time restricting analyses to data from test runs in which accuracy on the Recency task was .67 or above. This restricted analysis resulted in a mean accuracy of .77 on the Recency task. At

Table 2
Prefrontal and parietal regions demonstrating greater activation during correct Recency vs. correct Novelty decisions

Region		MNI coordinates			∼BA	*Z*-score
L	Intraparietal sulcus	−30	−60	48	7	4.06
L	Frontopolar cortex	−24	57	9	10	3.54
L	Mid. dorsolateral PFC	−42	24	27	9/46	4.22
L	Post. dorsolateral PFC/premotor	−30	9	51	6/8	3.56
R	Superior frontal cortex	33	15	60	6	3.57
		27	27	60	8	3.57
		30	30	54	8	3.53
		33	18	66	6	3.52
L	Medial frontal cortex	−3	15	51	6	4.55
		−6	24	45	8	4.43
R	Medial frontal cortex	12	30	36	8	4.01

Analyses were thresholded at $p < .001$, uncorrected. A list of all coordinates is available from the authors upon request. ∼BA: approximate Brodmann's area; L: left; R: right; Mid.: middle; Post.: posterior.

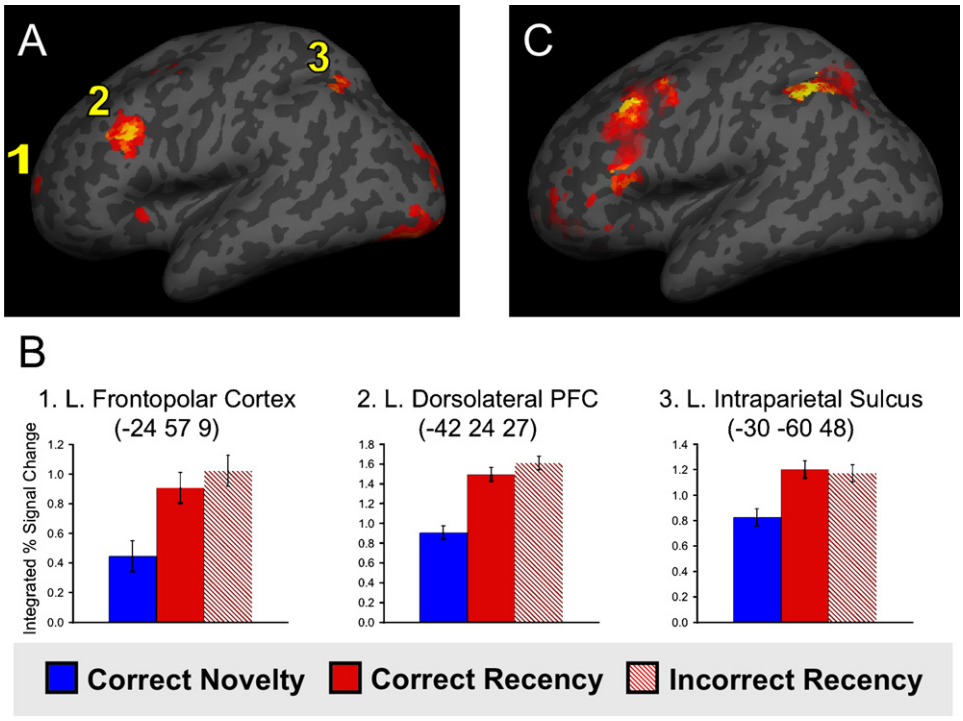

Fig. 2. (A) Regions demonstrating greater activation for correct Recency trials in comparison to correct Novelty trials, rendered on a canonical inflated brain. (B) The bar graphs show integrated percent signal change (area under the observed hemodynamic response function from 4 to 10 s post-stimulus onset) from selected regions of interest (ROIs). Data from incorrect Novelty trials are not plotted due to an insufficient number of trials. MNI coordinates are listed for each ROI. (C) Regions demonstrating greater activation for domain-general source recollection in comparison to novelty detection (from Dobbins & Wagner, 2005), rendered on a canonical inflated brain.

the neural level, we again compared correct Recency trials to correct Novelty trials, but at a slightly more liberal threshold ($p < .005$) given that power was reduced because fewer trials contributed to the analysis (30.8 for correct Recency; 25.3 for correct Novelty). Importantly, this restricted analysis revealed Recency-related activation in the same left FPC, dorsolateral PFC, and intraparietal regions as in the unrestricted analysis, with no new regions being detected.

Extracting the observed hemodynamic response functions from the left-lateralized a priori expected regions and submitting the resulting percent signal change data to ANOVA revealed that none of these regions showed a reliable difference between successful and unsuccessful Recency trials (Fs < 2.47; ps > .10; Fig. 2B), with both types of Recency trials resulting in greater activation relative to correct Novelty trials (Fs > 7.29; ps < .001). Similarly, the right superior frontal region did not show a reliable difference between successful and unsuccessful Recency trials ($F(1,17) = 1.99$, $p > .10$). When this analysis was performed on the restricted fMRI data (where mean Recency accuracy was .77), we again failed to observe a reliable difference between successful and unsuccessful Recency trials (Fs < 2.83; ps > .10), suggesting that the absence of such an effect in left frontal and parietal regions is not a byproduct of contamination of the correct Recency condition by guesses. Accordingly, the mechanisms subserved by left FPC, dorsolateral PFC, and intraparietal sulcus were differentially engaged when retrieval was oriented towards assessing recency relative to detecting novelty, irrespective of retrieval success.

Since Recency decisions took longer than Novelty decisions, we also examined whether the magnitude of the Recency > Novelty effect in any of these lateral PFC and parietal regions correlated with response latency. For each region, we computed between-subject correlations between the difference in percent signal change and in reaction time on correct Recency and Novelty trials. These correlations were not significant for the left fronto-parietal regions (ps > .10), but proved reliable for the right superior frontal region ($R^2 = .31$, $p < .05$).

3.2.2. *Relation between temporal recency and source recollection effects*

Consideration of the pattern of activation observed in the Recency > Novelty comparison suggests that it is similar to a network of left fronto-parietal regions previously identified to show greater activation when subjects make source recollection versus novelty detection decisions (Fig. 2C; Dobbins & Wagner, 2005; see also, Dobbins et al., 2002, 2003; Ranganath et al., 2000). To directly assess the overlap of regions observed in the present Recency > Novelty comparison with that in the Source > Novelty comparison of Dobbins and Wagner (2005), we rendered the conjunction of these two effects (each thresholded at $p < .001$). Notably, even though the two studies differed along a number of dimensions – independent subject samples, distinct incidental encoding tasks, and word (present) versus object (D&W) retrieval cues – this comparison revealed overlap between these retrieval effects in mid-dorsolateral PFC, medial superior frontal cortex, and intraparietal sulcus (Fig. 3). In addition, the present

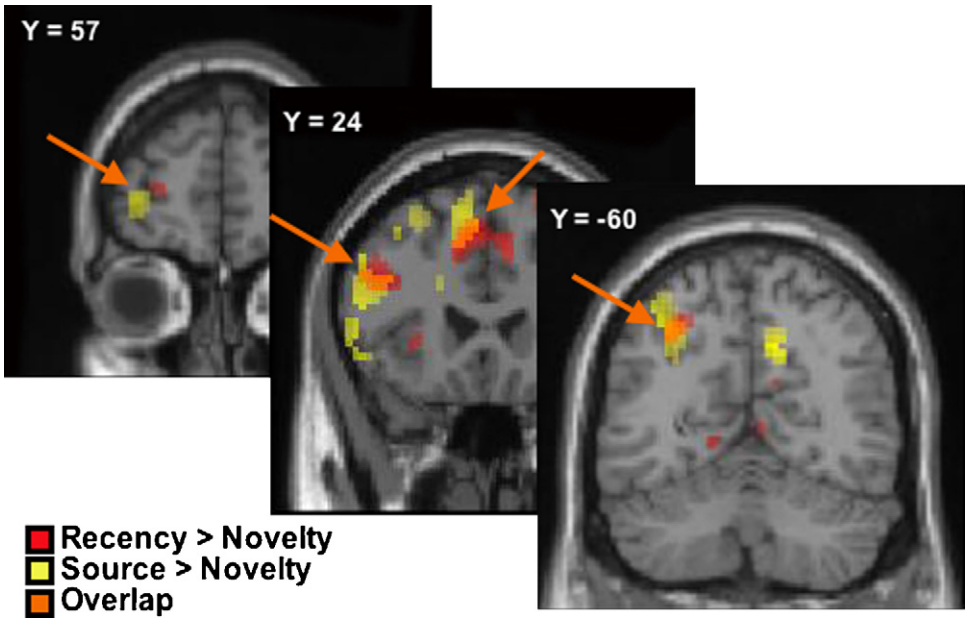

Fig. 3. A conjunction analysis assessed the overlap between regions showing greater activation during recency decisions vs. novelty detection with those showing greater activation during source recollection vs. novelty detection. The latter source recollection data were defined as demonstrating greater activation for both conceptual and perceptual source recollection judgments compared with novelty detection (from Dobbins & Wagner, 2005).

Recency > Novelty response in left FPC fell just medial to that observed in the Source > Novelty comparison. Accordingly, the left-lateralized regions in the present study of temporal recency decisions appear to be a subset of those observed in prior studies when subjects are instructed to attempt to recollect contextual details. While this conjunction analysis must be interpreted with caution because the co-localized effects need not reflect overlapping mnemonic processes, it is important to emphasize that this analysis revealed a *set* of brain regions (rather than a single region) that overlaps when subjects make Recency versus Novelty and Source versus Novelty judgments. As argued by Poldrack (2006), "the analysis of sets of regions . . . might provide greater selectivity than the analysis of single brain regions, to the degree that specific processes engage specific networks" (p. 62). As such, this conjunction suggests that one potential difference between the Recency and Novelty trials is that participants were attempting to recollect contextual details to guide their recency decisions.

3.2.3. Recency success analysis

While none of the frontal and parietal regions observed in the Recency > Novelty contrast showed a recency success effect, it remains possible that other structures might have demonstrated such a pattern. A voxel-level analysis that directly contrasted correct and incorrect Recency trials revealed no regions that were positively modulated by recency success at a standard statistical threshold ($p < .001$). However, lowering the threshold to a slightly more liberal level ($p < .005$) revealed greater activation during correct versus incorrect Recency trials in right posterior hippocampus (MNI coordinates: 30, −36, −3). Given prior observations that successful recollection is accompanied by increased hippocampal activity (e.g., Dobbins et al., 2003; Eldridge et al., 2000; Yonelinas, Otten, Shaw, & Rugg, 2005), this observation further suggests that subjects attempted to recollect contextual details to guide their Recency decisions.

The reverse pattern of activation (Recency incorrect > correct) was observed in several regions (Table 3), including bilateral anterior cingulate cortex (ACC). A similar pattern of ACC activation, along with a response in right dorsolateral PFC, was observed by Dobbins et al. (2003) when comparing incorrect versus correct temporal recency decisions. In a related study, Bunge, Burrows, & Wagner (2004) observed that ACC activation may be associated with the conflict that arises during episodic retrieval attempts when one is forced to choose between items of similar familiarity in the absence of recollection. As proposed at the outset and as suggested by the differential posterior hippocampus activation on successful versus unsuccessful Recency trials, in the present experiment it is likely that on incorrect Recency trials subjects failed to recollect relevant contextual details and thus attempted (and

Table 3
Regions demonstrating greater activation during incorrect Recency vs. correct Recency decisions

Region		MNI coordinates			~BA	Z-Score
R	Superior frontal cortex	12	9	69	6	3.81
		9	27	57	8	3.25
L	Superior frontal cortex	−9	3	72	6	3.64
R	Ant. cingulate cortex	9	24	42	32	3.61
L	Ant. Cingulate Cortex	−6	27	33	32	3.36
		−9	18	42	32	3.31
L	Post. ventrolateral PFC	−48	12	12	44	3.47
L	Medial frontal cortex	−3	30	42	8	3.23
R	Insular cortex	42	9	0	13	3.32

Analyses were thresholded at $p < .001$, uncorrected. ~BA: approximate Brodmann's area; L: left; R: right; Ant.; anterior; Post.: posterior.

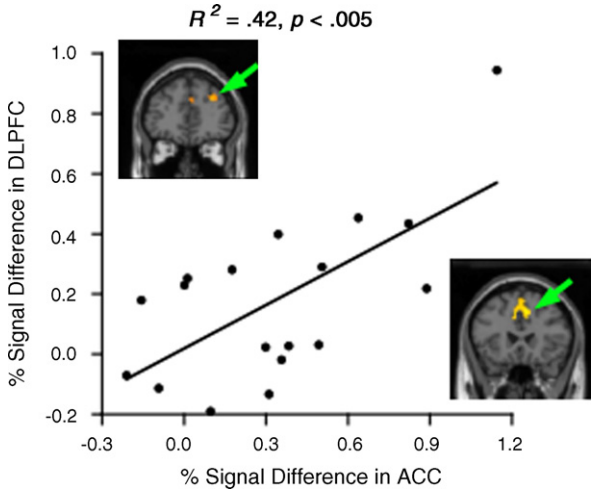

Fig. 4. Regression plot displaying the integrated percent signal change difference between incorrect and correct Recency trials for right dorsolateral PFC relative to ACC. Activation differences in these two ROIs were positively correlated.

ultimately failed) to discriminate between the two studied items on the basis of differential trace strength/familiarity. From this perspective, demands on familiarity monitoring would be greater during incorrect versus correct Recency trials, perhaps resulting in a parallel retrieval situation as in the Bunge et al. study. Notably, Bunge et al. also observed that ACC activation was positively correlated with that in right dorsolateral PFC, consistent with findings from Henson et al. (1999) that suggest that right dorsolateral PFC activation is greater on trials in which demands on the monitoring of item familiarity are high.

Motivated by the observations of Dobbins et al. (2003), Bunge et al. (2004), and Henson et al. (1999), we sought to determine whether right dorsolateral PFC tended to show a greater response during incorrect versus correct Recency trials, and, if so, whether the magnitude of this effect correlated with that in ACC. Consistent with this possibility, when we adopted a slightly more liberal threshold ($p < .005$) for the incorrect > correct Recency contrast, an effect was observed in right dorsolateral PFC (MNI coordinates: 33, 42, 33; ~BA 9), with no corresponding effect in the MTL. Analysis of percent signal change in right ACC and dorsolateral PFC revealed that the magnitude of the incorrect > correct Recency effect in ACC was positively correlated with that in dorsolateral PFC ($R^2 = .42$, $p < .005$; Fig. 4). When the subject with the highest ACC and dorsolateral PFC activation was excluded from the analysis, a trend for a relation between activation in ACC and dorsolateral PFC remained ($R^2 = .21$, $p = .066$).

3.2.4. Goal-dependent modulation of MTL novelty activity

As a final objective, we sought to determine if any regions were more active when the mnemonic goal was to detect Novelty versus assess relative Recency. In particular, we were interested in whether the commonly observed differential response to novelty within the MTL (e.g., Dolan & Fletcher, 1997; Habib et al., 2003; Kirchhoff et al., 2000; Knight, 1996; O'Kane et al., 2005; Saykin et al., 1999; Stark & Squire, 2001; Stern et al., 1996; Tulving et al., 1996) might be modulated depending on the subject's mnemonic goal. Although the retrieval probes were identical across Novelty and Recency trials, with only the retrieval goal differing, comparison of Novelty versus Recency trials revealed activation in multiple regions, including effects in lateral prefrontal cortices and regions within the MTL. Specifically, greater activation on Novelty trials was observed in left dorsolateral (~BA 9/46) and posterior ventrolateral PFC (~BA 44), as well as in right ventrolateral PFC (~BA 44/45/47) (Fig. 5A; Table 4). It is worth noting that this left dorsolateral PFC response is anatomically distinct from that observed in prior studies of source recollection (e.g., see Fig. 2C), and is, by definition, distinct from that showing a greater response on Recency versus Novelty trials in the present experiment (Fig. 2A). Importantly, when this analysis was recomputed on the restricted test phase data, where mean Recency accuracy was .77, the voxel-level comparison of Novelty versus Recency trials again revealed activation in these same left dorsolateral and bilateral ventrolateral PFC regions (thresholded at $p < .005$).

Within the MTL, greater activation on Novelty versus Recency trials was present in several regions: left anterior hippocampus/entorhinal cortex, left posterior parahippocampal cortex, and right entorhinal cortex (Fig. 5B; Table 4). At the acquired functional resolution, it is difficult to definitively discern entorhinal cortex from the medial extent of perirhinal cortex, and thus the right entorhinal focus may include a portion of perirhinal cortex (a Novelty > Recency pattern was also observed in right anterior fusiform cortex, which may partially encompass lateral perirhinal cortex; Table 4). Interestingly, when we extracted the observed percent signal change from these left and right MTL regions, the left posterior parahippocampal region showed a reliable difference between successful and unsuccessful Recency trials ($F(1,17) = 14.69$; $p = .001$; Fig. 5B), a pattern that parallels the posterior hippocampal Recency success observation discussed above. By contrast, the left anterior hippocampal/entorhinal and right entorhinal regions did not differ according to Recency success (Fs < 1). Finally, the recomputed voxel-level analysis of Novelty versus Recency trials, restricted to higher accuracy Recency test runs, revealed that bilateral anterior hippocampal regions were differentially activate during Novelty versus Recency decisions (thresholded at $p < .005$). The left anterior hippocampal region overlapped the left hippocampal region observed in the unrestricted analysis, whereas the right anterior hippocampal region (MNI coordinates: 21, −12, −15) overlapped, but was slightly more anterior and dorsal to, the right entorhinal region from the unrestricted analysis. Collectively, these findings suggest that on Novelty trials participants may have differentially oriented attention to the novel stimulus, thus enhancing MTL novelty encoding processes. That is, novelty-related MTL responses are not obligatory, but rather are gated by attention and task demands.

Further consideration of the activation patterns seen in regions showing a Novelty > Recency effect revealed that activation levels tended to fall below the arrows-task baseline on Recency trials and then returned to or exceeded (in some

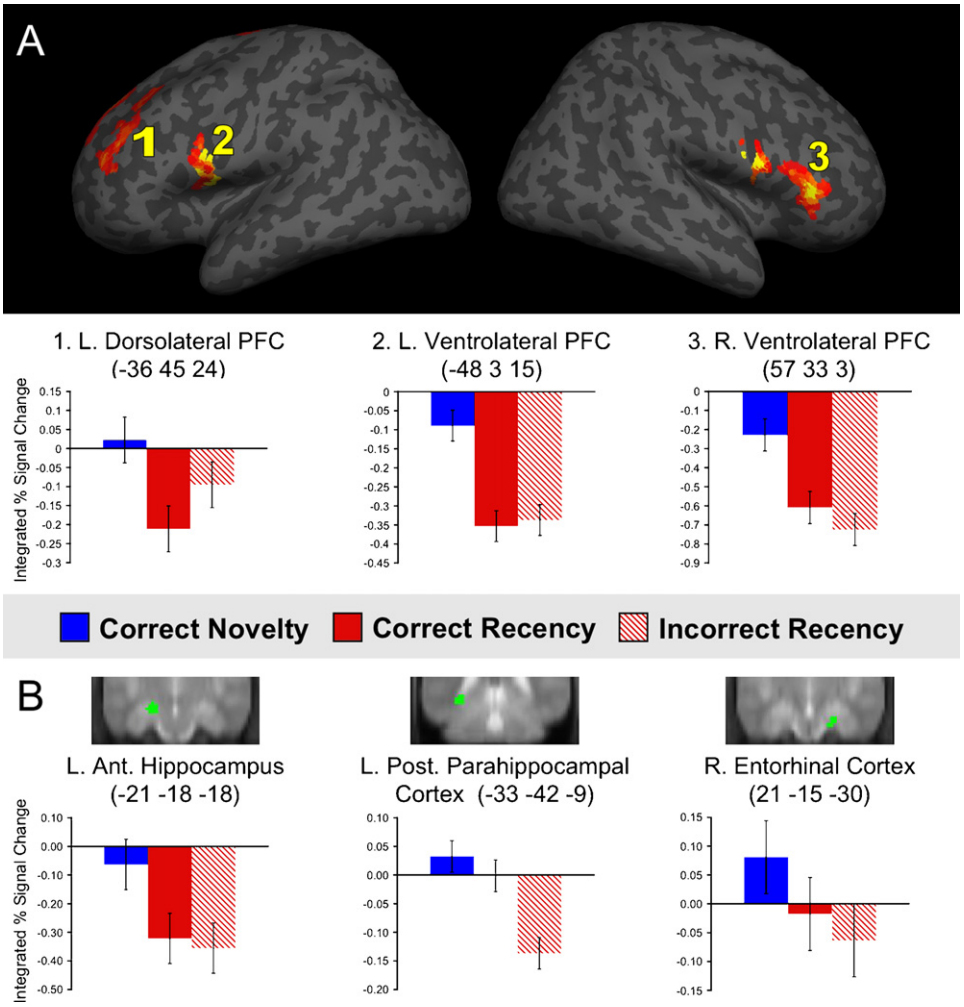

Fig. 5. Frontal and medial temporal regions demonstrating greater activation during correct Novelty vs. correct Recency trials. The bar graphs show integrated percent signal change from selected ROIs. (A) Lateral PFC regions showing this effect are rendered on a canonical inflated brain, with the observed condition-specific activation levels plotted below. (B) Medial temporal ROIs are displayed in green on group averaged T2 anatomical images, with condition-specific activation levels plotted below.

instances) baseline on Novelty trials (Fig. 5). Given this pattern, we explored whether the Novelty > Recency pattern might stem from there being more time to engage in non-task related cognition in the Novelty trials due to the faster reaction times in this condition. Specifically, since Novelty decisions took less time than Recency decisions, the greater neural activation during Novelty trials may reflect processes that were engaged during time spent off task (Binder et al., 1999; Shulman et al., 1997; Stark & Squire, 2001). When we divided our participants into two groups – those with relatively fast Novelty reaction times

Table 4
Lateral prefrontal and medial temporal lobe regions demonstrating greater activation during correct Novelty vs. correct Recency decisions

Region		MNI coordinates			~BA	*Z*-score
L	Ant. dorsolateral PFC	−36	45	24	46	3.92
L	Mid. dorsolateral PFC	−27	24	36	9	3.69
L	Post. ventrolateral PFC	−48	3	15	44	6.04
R	Ant. ventrolateral PFC	57	33	3	45/47	4.94
R	Post. ventrolateral PFC	63	15	9	44	5.28
L	Ant. hippocampus/entorhinal cortex	−21	−18	−18	27/34	3.61
L	Post. parahippocampal cortex	−33	−42	−9	35/36/19	4.69
R	Entorhinal cortex	21	−15	−30	28/34	3.51
R	Ant. fusiform cortex	30	−3	−48	20	3.84

Analyses were thresholded at $p < .001$, uncorrected. A list of all coordinates is available from the authors upon request. ~BA: approximate Brodmann's area; L: left; R: right; Ant.: anterior; Mid.: middle; Post.: posterior.

versus those with relatively slow Novelty reaction times – the percent signal change data from these lateral PFC and MTL regions did not significantly differ across groups ($ps > .05$), arguing against such an interpretation. Nevertheless, to further test the possibility that the greater activation during Novelty trials reflects time spent off task, we conducted several additional analyses that examined whether the Novelty > Recency pattern was correlated with reaction time. First, we computed between-subject correlations between the difference in Novelty versus Recency activation levels and in reaction time, assessing these correlations both at the voxel level and the region level. At the voxel level, none of the aforementioned lateral PFC or MTL regions correlated with mean reaction time differences even at the extremely liberal threshold of $p < .10$. At the region level, the Novelty > Recency activation pattern was uncorrelated with reaction time in the majority of regions ($ps > .10$), with only the left ventrolateral PFC region showing a significant correlation ($R^2 = .25$, $p = .051$). However, this correlation in left ventrolateral PFC was negative, indicating that increased time spent on the Novelty trials was associated with greater activation, ruling out a "time off task" explanation.

In a final analysis, within-subject, between-trial variance due to reaction time was modeled by using trial reaction time as a nuisance covariate in the GLM. Specifically, reaction time was modeled as a parametrically-modulated epoch using trial-specific reaction times for each subject, thus allowing a test for condition-specific effects that cannot be explained by reaction time differences. Importantly, when factoring out signal variance due to reaction time, the same lateral PFC and MTL regions were differentially activated on Novelty trials in comparison to Recency trials. Specifically, the Novelty > Recency pattern was present in left dorsolateral PFC and bilateral ventrolateral PFC at the standard threshold ($p < .001$), and in left posterior parahippocampal cortex and right entorhinal cortex at a slightly more liberal threshold ($p < .005$). This effect also was apparent in left anterior hippocampus/entorhinal cortex, though at a more relaxed threshold ($p < .01$); accordingly, we suggest caution is warranted regarding whether differential activation was present in hippocampus proper.

Collectively, while we cannot definitively rule out the possible role of reaction time differences in Novelty > Recency activation patterns in lateral PFC and MTL cortices, the preceding analyses suggest that reaction time had a limited impact on this activation pattern. According, we propose that the observed Novelty-related responses in MTL and PFC reflect a goal-directed attentional orienting to novel test probes, modulating novelty effects within the MTL and elsewhere.

3.2.5. Functional consequences of attention-gated novelty processing

To assess whether the goal-directed gating of MTL novelty responses carries a functional consequence for novelty encoding, we conducted a follow-up behavioral study with an independent sample of participants ($N = 12$). In this study, participants underwent the identical behavioral procedures as in the fMRI study but with the addition of an unexpected subsequent recognition memory test that included 48 items that had served as novel probes during the Recency trials, 48 items that had served as novel probes during the Novelty trials, along with 96 foils (i.e., items not previously encountered). The results from this subsequent test confirmed that participants were more likely to later recognize the novel items from the Novelty trials (.68) than the novel items from the Recency trials (.44; $t(11) = 5.25$, $p < .0005$); the false alarm rate was .26. This finding suggests that the differential MTL activation observed during Novelty versus Recency trials in the present fMRI study may have reflected not only increased attention to the novel items but also enhanced encoding of these test probes.

4. Discussion

Declarative memory supports the encoding and retrieval of information about what items were experienced, as well as information that can serve to guide judgments about when items were experienced. While much is known about the neural mechanisms supporting item recognition (Aggleton & Brown, 2006; Rugg & Yonelinas, 2003; Wheeler & Buckner, 2004), the neural underpinnings of temporal-order retrieval remain relatively under specified. The present fMRI study used matched test conditions to investigate the neural processes engaged during temporal recency and novelty detection decisions. There were four main findings. First, we observed that a network of left-lateralized regions, including FPC, dorsolateral PFC, and intraparietal sulcus, was differentially active during temporal recency decisions compared with novelty detection. Second, a conjunction analysis revealed that these left-lateralized regions overlapped with those previously observed to be engaged during source recollection versus novelty detection. Third, correct Recency decisions activated posterior hippocampus and parahippocampal cortex, whereas incorrect Recency decisions elicited greater ACC activation; the magnitude of this latter effect positively correlated with activation in right dorsolateral PFC. Finally, correct Novelty decisions activated the anterior MTL to a greater extent than did correct Recency decisions. Below we discuss the theoretical implications of these findings, as well as their relation to the broader literature on PFC and MTL contributions to declarative memory.

4.1. Temporal recency and contextual recollection

Relative to novelty decisions, judgments of temporal recency elicited greater activation in a set of left-lateralized PFC and parietal regions, with the particular left fronto-parietal regions engaged during recency judgments overlapping with regions previously reported to be selectively activated during attempts to recollect contextual details about a past encounter (Cansino et al., 2002; Dobbins et al., 2002, 2003; Dobbins & Wagner, 2005; Kahn, Davachi, & Wagner, 2004; Ranganath et al., 2000). This inter-experimental overlap suggests that the participants in the present study were attempting to recollect contextual details to guide their recency decisions. While this conclusion constitutes a reverse inference, it is worth noting that this inference rests on inter-experiment overlap of a *set* of brain regions (rather than simply a single region). Moreover, con-

sistent with this inference, the present data revealed that right posterior hippocampus and left parahippocampal cortex demonstrated greater activation during successful versus unsuccessful Recency decisions. Accordingly, although temporal recency decisions often depend on monitoring relative trace strength or item familiarity (Dobbins et al., 2003; Mitchell, Johnson, Raye, & Greene, 2004; Rajah & McIntosh, 2006), the present data indicate that, at least under some conditions, subjects may also attempt to recollect contextual details in the service of recency decisions (Curran & Friedman, 2003; Konishi et al., 2002; Suzuki et al., 2002).

4.2. Prefrontal cortex and temporal recency decisions

In contrast to the present left-lateralized PFC activity during correct Recency versus Novelty trials, previous neuroimaging studies have reported a preferential role of right FPC and dorsolateral PFC during temporal recency retrieval compared to item recognition (Cabeza et al., 1997, 2000) and to conceptual source recollection (Dobbins et al., 2003). One interpretation of right dorsolateral PFC activation during episodic retrieval is that it is associated with familiarity monitoring processes, especially when trace strength levels are near one's decision criterion (Henson et al., 1999). From this perspective, right dorsolateral PFC is differentially engaged when stimulus-based evidence along mnemonic or non-mnemonic dimensions must be evaluated in relation to a decision criterion, with such evidence-based monitoring demands increasing the closer the evidence falls to criterion (Henson et al., 1999; Rugg, Henson, & Robb, 2003; for related findings, see Fleck et al., 2006; Wagner, Desmond, Glover, & Gabrieli, 1998). Alternatively, Dobbins and Han (2006) propose that dorsolateral PFC activation may reflect rule-based rather than evidence-based decision processes, with activation tracking the number of stimulus classifications required for performance.

When we compared correct Recency to correct Novelty trials, we did not observe differential activation in right dorsolateral PFC nor right FPC. However, right dorsolateral PFC did demonstrate greater activation on incorrect compared to correct Recency trials, with the magnitude of this effect positively correlating with that in ACC (Fig. 4). This pattern is consistent with the prediction that mnemonic or response conflict would be differentially present on incorrect Recency trials, which in turn would increase monitoring, selection, or decision demands. These increased demands presumably occurred on incorrect Recency trials because, in the absence of contextual recollection, participants were forced to select between two alternatives that had similar levels of familiarity. Indeed, as with previous studies that observed right dorsolateral PFC activation during episodic retrieval conditions associated with familiarity monitoring processes, response latencies were significantly longer on incorrect versus correct Recency trials, suggesting that on incorrect Recency trials participants were engaged in effortful monitoring processes that required additional decision time (Gallo, Kensinger, & Schacter, 2006; Wheeler & Buckner, 2004). Although this difference in reaction time does not provide definitive evidence that participants differentially engaged in familiarity monitoring processes on incorrect Recency trials, the present fMRI data also revealed that activation in posterior hippocampus and parahippocampal cortex was weaker on incorrect than correct Recency trials, suggesting that recollection differed across these conditions. Moreover, the coupled change in dorsolateral PFC and ACC activation (Fig. 4) parallels other reports of functional coupling between ACC and dorsolateral PFC activation (Gehring & Knight, 2000), including under conditions where recollection fails and participants must select between two equally familiar stimuli (Bunge et al., 2004) (for related right dorsolateral PFC-ACC correlations, see Badre & Wagner, 2004; Kondo, Osaka, & Osaka, 2004).

4.3. Temporal recency, novelty, and the MTL

Activation in the hippocampus and posterior parahippocampal cortex has been previously associated with recollection of contextual details (Cansino et al., 2002; Eldridge et al., 2000; Wheeler & Buckner, 2004; Yonelinas et al., 2005). The present data demonstrate that posterior MTL responses can be differentially modulated by successful versus unsuccessful Recency decisions, suggesting that these Recency success effects reflect successful attempts to recollect stimulus-specific contextual details. This finding concurs with previous rodent and some human neuropsychological data indicating that the MTL plays an important role in memory for temporal-order (Downes et al., 2002; Fortin et al., 2002; Kesner et al., 2002; Kopelman et al., 1997; Mayes et al., 2001), and builds on previous fMRI studies that have observed MTL recruitment during relative recency decisions (Konishi et al., 2006, 2002). It is possible that the hippocampus is particularly necessary for temporal-order decisions when such decisions cannot be based on differential item familiarity (due to test items having similar levels of familiarity), as such conditions would require contextual recollection for successful performance. While further investigation is necessary to address this possibility, it may provide a partial account for why human MTL damage results in variable consequences for temporal-order memory (Downes et al., 2002; Hopkins et al., 1995; Kopelman et al., 1997; Mayes et al., 2001; Sagar et al., 1990).

The present data also indicate that MTL responses can be modulated by one's mnemonic goal and task demands. The recruitment of MTL regions during novelty detection is not uncommon (e.g., Dolan & Fletcher, 1997; Habib et al., 2003; Kirchhoff et al., 2000; Knight, 1996; O'Kane et al., 2005; Saykin et al., 1999; Stark & Squire, 2001; Stern et al., 1996; Tulving et al., 1996). What is striking in the present data is the demonstration that MTL activation was influenced by retrieval goals, rather than stimulus attributes, with activation being greater during Novelty trials compared to Recency trials. Because the retrieval probes were held constant between the Recency and Novelty tasks, this difference in MTL activation must be attributed to strategic differences in attentional orienting at retrieval. During Recency decisions, subjects are likely to have differentially oriented attention towards the familiar probes in attempts to trigger recollection of stimulus-specific contextual details and/or to

assess relative levels of familiarity. By contrast, during Novelty decisions, subjects are likely to have differentially oriented attention towards the novel probe.

While it remains possible that activation during the Novelty trials reflects neural processes engaged during time off task, the behavioral companion study provides evidence that is more consistent with the interpretation that this MTL response reflects increased processing of the novel probes encountered during Novelty trials, since these items were subsequently better remembered than the novel probes seen during Recency trials. Such attentional modulation of MTL responses complements recent demonstrations that when subjects attentionally select against an item at encoding, activation decreases in parahippocampal cortex and subsequent explicit memory performance is poor (Dudukovic & Wagner, 2006; Gazzaley, Cooney, McEvoy, Knight, & D'Esposito, 2005; Yi & Chun, 2005). Important issues for future research include (a) elucidating how such modulation occurs (e.g., via fronto-parietal mechanisms directly influencing MTL function or indirectly via fronto-parietal modulation of representations in posterior neocortical structures), and (b) determining whether there are conditions under which MTL encoding and retrieval responses are obligatory or whether MTL mechanisms are always modulated by the goal-directed allocation of attention.

4.4. Conclusion

Temporal context facilitates the integration of life events into meaningful episodes. The present data expand our understanding of mechanisms that support memory decisions about temporal recency, demonstrating that recency decisions engage (a) fronto-parietal neural processes often recruited during attempts to recollect contextual details, with (b) the additional elicitation of processes supporting the assessment or monitoring of stimulus familiarity, especially when contextual recollection fails. The present data also illustrate that our mnemonic goals at retrieval impact processing in multiple structures, including the MTL memory system. Such goals not only influence what is remembered in the present, but also what is encoded during these acts of memory. As such, how we work with memory in the present can have long-term consequences for what will be remembered in the future.

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References

Aggleton, J. P., & Brown, M. W. (1999). Episodic memory, amnesia, and the hippocampal-anterior thalamic axis. *Behavioral and Brain Sciences*, *22*(3), 425–444.

Aggleton, J. P., & Brown, M. W. (2006). Interleaving brain systems for episodic and recognition memory. *Trends in Cognitive Sciences*, *10*(10), 455–463.

Badre, D., & Wagner, A. D. (2004). Selection, integration, and conflict monitoring; assessing the nature and generality of prefrontal cognitive control mechanisms. *Neuron*, *41*(3), 473–487.

Binder, J. R., Frost, J. A., Hammeke, T. A., Bellgowan, P. S., Rao, S. M., & Cox, R. W. (1999). Conceptual processing during the conscious resting state. A functional MRI study. *Journal of Cognitive Neuroscience*, *11*(1), 80–95.

Bunge, S. A., Burrows, B., & Wagner, A. D. (2004). Prefrontal and hippocampal contributions to visual associative recognition: Interactions between cognitive control and episodic retrieval. *Brain & Cognition*, *56*(2), 141–152.

Cabeza, R., Anderson, N. D., Houle, S., Mangels, J. A., & Nyberg, L. (2000). Age-related differences in neural activity during item and temporal-order memory retrieval: A positron emission tomography study. *Journal of Cognitive Neuroscience*, *12*(1), 197–206.

Cabeza, R., Mangels, J., Nyberg, L., Habib, R., Houle, S., McIntosh, A. R., et al. (1997). Brain regions differentially involved in remembering what and when: A PET study. *Neuron*, *19*(4), 863–870.

Cansino, S., Maquet, P., Dolan, R. J., & Rugg, M. D. (2002). Brain activity underlying encoding and retrieval of source memory. *Cerebral Cortex*, *12*(10), 1048–1056.

Curran, T. (2000). Brain potentials of recollection and familiarity. *Memory and Cognition*, *28*(6), 923–938.

Curran, T., & Friedman, W. J. (2003). Differentiating location- and distance-based processes in memory for time: An ERP study. *Psychonomic Bulletin & Review*, *10*(3), 711–717.

Dobbins, I. G., Foley, H., Schacter, D. L., & Wagner, A. D. (2002). Executive control during episodic retrieval: Multiple prefrontal processes subserve source memory. *Neuron*, *35*(5), 989–996.

Dobbins, I. G., & Han, S. (2006). Isolating rule- versus evidence-based prefrontal activity during episodic and lexical discrimination: A functional magnetic resonance imaging investigation of detection theory distinctions. *Cerebral Cortex*, *16*(11), 1614–1622.

Dobbins, I. G., Rice, H. J., Wagner, A. D., & Schacter, D. L. (2003). Memory orientation and success: Separable neurocognitive components underlying episodic recognition. *Neuropsychologia*, *41*(3), 318–333.

Dobbins, I. G., & Wagner, A. D. (2005). Domain-general and domain-sensitive prefrontal mechanisms for recollecting events and detecting novelty. *Cerebral Cortex*, *15*(11), 1768–1778.

Dolan, R. J., & Fletcher, P. C. (1997). Dissociating prefrontal and hippocampal function in episodic memory encoding. *Nature*, *388*(6642), 582–585.

Downes, J. J., Mayes, A. R., MacDonald, C., & Hunkin, N. M. (2002). Temporal order memory in patients with Korsakoff's syndrome and medial temporal amnesia. *Neuropsychologia*, *40*(7), 853–861.

Dudukovic, N. M., & Wagner, A. D. (2006). Attending to remember and remembering to attend. *Neuron*, *49*(6), 784–787.

Duzel, E., Yonelinas, A. P., Mangun, G. R., Heinze, H. J., & Tulving, E. (1997). Event-related brain potential correlates of two states of conscious awareness in memory. *Proceedings of the National Academy of Sciences of the United States of America*, *94*(11), 5973–5978.

Eldridge, L. L., Knowlton, B. J., Furmanski, C. S., Bookheimer, S. Y., & Engel, S. A. (2000). Remembering episodes: A selective role for the hippocampus during retrieval. *Nature Neuroscience*, *3*(11), 1149–1152.

Eyler Zorrilla, L. T., Aguirre, G. K., Zarahn, E., Cannon, T. D., & D'Esposito, M. (1996). Activation of the prefrontal cortex during judgments of recency: A functional MRI study. *Neuroreport*, *7*(15–17), 2803–2806.

Fleck, M. S., Daselaar, S. M., Dobbins, I. G., & Cabeza, R. (2006). Role of prefrontal and anterior cingulate regions in decision-making processes shared by memory and nonmemory tasks. *Cerebral Cortex*, *16*(11), 1623–1630.

Fortin, N. J., Agster, K. L., & Eichenbaum, H. B. (2002). Critical role of the hippocampus in memory for sequences of events. *Nature Neuroscience*, *5*(5), 458–462.

Gallo, D. A., Kensinger, E. A., & Schacter, D. L. (2006). Prefrontal activity and diagnostic monitoring of memory retrieval: FMRI of the criterial recollection task. *Journal of Cognitive Neuroscience*, *18*(1), 135–148.

Gazzaley, A., Cooney, J. W., McEvoy, K., Knight, R. T., & D'Esposito, M. (2005). Top-down enhancement and suppression of the magnitude and speed of neural activity. *Journal of Cognitive Neuroscience*, *17*(3), 507–517.

Gehring, W. J., & Knight, R. T. (2000). Prefrontal-cingulate interactions in action monitoring. *Nature Neuroscience*, *3*(5), 516–520.

Glover, G. H., & Law, C. S. (2001). Spiral-in/out BOLD FMRI for increased SNR and reduced susceptibility artifacts. *Magnetic Resonance in Medicine*, *46*(3), 515–522.

Gonsalves, B. D., Kahn, I., Curran, T., Norman, K. A., & Wagner, A. D. (2005). Memory strength and repetition suppression: Multimodal imaging of medial temporal cortical contributions to recognition. *Neuron*, *47*(5), 751–761.

Habib, R., McIntosh, A. R., Wheeler, M. A., & Tulving, E. (2003). Memory encoding and hippocampally-based novelty/familiarity discrimination networks. *Neuropsychologia*, *41*(3), 271–279.

Henson, R. N., Rugg, M. D., Shallice, T., & Dolan, R. J. (2000). Confidence in recognition memory for words: Dissociating right prefrontal roles in episodic retrieval. *Journal of Cognitive Neuroscience*, *12*(6), 913–923.

Henson, R. N., Shallice, T., & Dolan, R. J. (1999). Right prefrontal cortex and episodic memory retrieval: A functional MRI test of the monitoring hypothesis. *Brain*, *122*(Pt 7), 1367–1381.

Hintzman, D. L. (2001). Judgments of frequency and recency: How they relate to reports of subjective awareness. *Journal of Experimental Psychology: Learning, Memory & Cognition*, *27*(6), 1347–1358.

Hintzman, D. L. (2003). Judgments of recency and their relation to recognition memory. *Memory & Cognition*, *31*(1), 26–34.

Hintzman, D. L. (2005). Memory strength and recency judgments. *Psychonomic Bulletin & Review*, *12*(5), 858–864.

Hopkins, R. O., Kesner, R. P., & Goldstein, M. (1995). Item and order recognition memory in subjects with hypoxic brain injury. *Brain & Cognition*, *27*(2), 180–201.

Kahn, I., Davachi, L., & Wagner, A. D. (2004). Functional-neuroanatomic correlates of recollection: Implications for models of recognition memory. *Journal of Neuroscience*, *24*(17), 4172–4180.

Kensinger, E. A., Clarke, R. J., & Corkin, S. (2003). What neural correlates underlie successful encoding and retrieval? A functional magnetic resonance imaging study using a divided attention paradigm. *Journal of Neuroscience*, *23*(6), 2407–2415.

Kesner, R. P., Gilbert, P. E., & Barua, L. A. (2002). The role of the hippocampus in memory for the temporal order of a sequence of odors. *Behavioral Neuroscience*, *116*(2), 286–290.

Kesner, R. P., Hopkins, R. O., & Fineman, B. (1994). Item and order dissociation in humans with prefrontal cortex damage. *Neuropsychologia*, *32*(8), 881–891.

Kirchhoff, B. A., Wagner, A. D., Maril, A., & Stern, C. E. (2000). Prefrontal-temporal circuitry for episodic encoding and subsequent memory. *Journal of Neuroscience*, *20*(16), 6173–6180.

Knight, R. (1996). Contribution of human hippocampal region to novelty detection. *Nature*, *383*(6597), 256–259.

Kondo, H., Osaka, N., & Osaka, M. (2004). Cooperation of the anterior cingulate cortex and dorsolateral prefrontal cortex for attention shifting. *Neuroimage*, *23*(2), 670–679.

Konishi, S., Asari, T., Jimura, K., Chikazoe, J., & Miyashita, Y. (2006). Activation shift from medial to lateral temporal cortex associated with recency judgements following impoverished encoding. *Cerebral Cortex*, *16*(4), 469–474.

Konishi, S., Uchida, I., Okuaki, T., Machida, T., Shirouzu, I., & Miyashita, Y. (2002). Neural correlates of recency judgment. *Journal of Neuroscience*, *22*(21), 9549–9555.

Kopelman, M. D., Stanhope, N., & Kingsley, D. (1997). Temporal and spatial context memory in patients with focal frontal, temporal lobe, and diencephalic lesions. *Neuropsychologia*, *35*(12), 1533–1545.

Mayes, A. R., Isaac, C. L., Holdstock, J. S., Hunkin, N. M., Montaldi, D., Downes, J. J., et al. (2001). Memory for single items, word pairs, and temporal order of different kinds in a patient with selective hippocampal lesions. *Cognitive Neuropsychology*, *18*(2), 97–123.

Milner, B., Corsi, P., & Leonard, G. (1991). Frontal-lobe contribution to recency judgements. *Neuropsychologia*, *29*(6), 601–618.

Mitchell, K. J., Johnson, M. K., Raye, C. L., & Greene, E. J. (2004). Prefrontal cortex activity associated with source monitoring in a working memory task. *Journal of Cognitive Neuroscience*, *16*(6), 921–934.

Nolde, S. F., Johnson, M. K., & D'Esposito, M. (1998). Left prefrontal activation during episodic remembering: An event-related FMRI study. *Neuroreport*, *9*(15), 3509–3514.

Norman, K. A., & O'Reilly, R. C. (2003). Modeling hippocampal and neocortical contributions to recognition memory: A complementary-learning-systems approach. *Psychological Review*, *110*(4), 611–646.

Nyberg, L., McIntosh, A. R., Cabeza, R., Habib, R., Houle, S., & Tulving, E. (1996). General and specific brain regions involved in encoding and retrieval of events: What, where, and when. *Proceedings of the National Academy of Sciences of the United States of America*, *93*(20), 11280–11285.

O'Kane, G., Insler, R. Z., & Wagner, A. D. (2005). Conceptual and perceptual novelty effects in human medial temporal cortex. *Hippocampus*, *15*(3), 326–332.

Poldrack, R. A. (2006). Can cognitive processes be inferred from neuroimaging data? *Trends in Cognitive Sciences*, *10*(2), 59–63.

Rajah, M. N., & McIntosh, A. R. (2006). Dissociating prefrontal contributions during a recency memory task. *Neuropsychologia*, *44*(3), 350–364.

Ranganath, C., Johnson, M. K., & D'Esposito, M. (2000). Left anterior prefrontal activation increases with demands to recall specific perceptual information. *Journal of Neuroscience*, *20*(22), RC108.

Ranganath, C., Yonelinas, A. P., Cohen, M. X., Dy, C. J., Tom, S. M., & D'Esposito, M. (2004). Dissociable correlates of recollection and familiarity within the medial temporal lobes. *Neuropsychologia*, *42*(1), 2–13.

Rugg, M. D., Fletcher, P. C., Chua, P. M., & Dolan, R. J. (1999). The role of the prefrontal cortex in recognition memory and memory for source: An FMRI study. *Neuroimage*, *10*(5), 520–529.

Rugg, M. D., Henson, R. N., & Robb, W. G. (2003). Neural correlates of retrieval processing in the prefrontal cortex during recognition and exclusion tasks. *Neuropsychologia*, *41*(1), 40–52.

Rugg, M. D., & Yonelinas, A. P. (2003). Human recognition memory: A cognitive neuroscience perspective. *Trends in Cognitive Sciences*, *7*(7), 313–319.

Sagar, H. J., Gabrieli, J. D., Sullivan, E. V., & Corkin, S. (1990). Recency and frequency discrimination in the amnesic patient H.M. *Brain*, *113*(Pt 3), 581–602.

Saykin, A. J., Johnson, S. C., Flashman, L. A., McAllister, T. W., Sparling, M., Darcey, T. M., et al. (1999). Functional differentiation of medial temporal and frontal regions involved in processing novel and familiar words: An FMRI study. *Brain*, *122*(Pt 10), 1963–1971.

Shimamura, A. P., Janowsky, J. S., & Squire, L. R. (1990). Memory for the temporal order of events in patients with frontal lobe lesions and amnesic patients. *Neuropsychologia*, *28*(8)

Shulman, G. L., Fiez, J. A., Corbetta, M., Buckner, R. L., Miezin, F. M., Raichle, M. E., et al. (1997). Common blood flow changes across visual tasks: II. Decreases in cerebral cortex. *Journal of Cognitive Neuroscience*, *9*(5), 648–663.

Squire, L. R., Stark, C. E., & Clark, R. E. (2004). The medial temporal lobe. *Annual Review of Neuroscience*, *27*, 279–306.

Stark, C. E., & Squire, L. R. (2001). When zero is not zero: The problem of ambiguous baseline conditions in FMRI. *Proceedings of the National Academy of Sciences of the United States of America*, *98*(22), 12760–12766.

Stern, C. E., Corkin, S., Gonzalez, R. G., Guimaraes, A. R., Baker, J. R., Jennings, P. J., et al. (1996). The hippocampal formation participates in novel picture encoding: Evidence from functional magnetic resonance imaging. *Proceedings of the National Academy of Sciences of the United States of America*, *93*(16), 8660–8665.

Suzuki, M., Fujii, T., Tsukiura, T., Okuda, J., Umetsu, A., Nagasaka, T., et al. (2002). Neural basis of temporal context memory: A functional MRI study. *Neuroimage*, *17*(4), 1790–1796.

Tendolkar, I., & Rugg, M. D. (1998). Electrophysiological dissociation of recency and recognition memory. *Neuropsychologia*, *36*(6), 477–490.

Tulving, E., Markowitsch, H. J., Craik, F. E., Habib, R., & Houle, S. (1996). Novelty and familiarity activations in PET studies of memory encoding and retrieval. *Cerebral Cortex*, *6*(1), 71–79.

Wagner, A. D., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. (1998). Prefrontal cortex and recognition memory. Functional-MRI evidence for context-dependent retrieval processes. *Brain*, *121*(Pt 10), 1985–2002.

Wheeler, M. E., & Buckner, R. L. (2004). Functional-anatomic correlates of remembering and knowing. *Neuroimage*, *21*(4), 1337–1349.

Yi, D. J., & Chun, M. M. (2005). Attentional modulation of learning-related repetition attenuation effects in human parahippocampal cortex. *Journal of Neuroscience*, *25*(14), 3593–3600.

Yonelinas, A. P. (2002). The nature of recollection and familiarity: A review of 30 years of research. *Journal of Memory and Language*, *46*(3), 441–517.

Yonelinas, A. P., Otten, L. J., Shaw, K. N., & Rugg, M. D. (2005). Separating the brain regions involved in recollection and familiarity in recognition memory. *Journal of Neuroscience*, *25*(11), 3002–3008.