The Short and Long of It: Neural Correlates of Temporal-order Memory for Autobiographical Events

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Abstract

■ Previous functional neuroimaging studies of temporal-order memory have investigated memory for laboratory stimuli that are causally unrelated and poor in sensory detail. In contrast, the present functional magnetic resonance imaging (fMRI) study investigated temporal-order memory for autobiographical events that were causally interconnected and rich in sensory detail. Participants took photographs at many campus locations over a period of several hours, and the following day they were scanned while making temporal-order judgments to pairs of photographs from different locations. By manipulating the temporal lag between the two locations in each trial, we compared the neural correlates associated with *reconstruction processes*, which we hypothesized depended on recollection and contribute mainly to short lags, and *distance processes*, which we hypothesized to depend on familiarity and contribute mainly to longer lags. Consistent with our hypotheses, parametric fMRI analyses linked shorter lags to activations in regions previously associated with recollection (left prefrontal, parahippocampal, precuneus, and visual cortices), and longer lags with regions previously associated with familiarity (right prefrontal cortex). The hemispheric asymmetry in prefrontal cortex activity fits very well with evidence and theories regarding the contributions of the left versus right prefrontal cortex to memory (recollection vs. familiarity processes) and cognition (systematic vs. heuristic processes). In sum, using a novel photo-paradigm, this study provided the first evidence regarding the neural correlates of temporal-order for autobiographical events. ■

INTRODUCTION

When we remember personally experienced past events, or episodic memory retrieval (Tulving, 1983), we usually retrieve not only *what* events happened (item memory) but also *when* they happened (temporal-order memory). Temporal-order memory is an important form of source memory (Johnson, Hashtroudi, & Lindsay, 1993) and an integral and defining characteristic of episodic memory (Wheeler, Stuss, & Tulving, 1997). Indeed, in many situations, episodic memories are useful only to the extent that temporal-order information is also available (e.g., remembering today's vs. yesterday's parking spot). Lesion (Milner, Corsi, & Leonard, 1991; Petrides, 1991; Milner, 1971) and functional neuroimaging (Cabeza et al., 1997; Eyler Zorilla, Aguirre, Zarahn, Cannon, & D'Esposito, 1996; Nyberg et al., 1996) studies have shown that the prefrontal cortex (PFC) is a critical region for temporal-order memory. There is also evidence of the important role of the medial-temporal lobes (MTL; Eichenbaum & Fortin, 2003; Downes, Mayes, MacDonald, & Hunkin, 2002; Konishi et al., 2002). However, the neural correlates of temporal-order memory, especially as they relate to autobiographical events, are not well understood. Ad-

dressing this issue was the goal of the present functional magnetic resonance imaging (fMRI) study.

It has been suggested that temporal-order memory for autobiographical memories involves both reconstruction and distance processes (Friedman, 1993, 2004). *Reconstruction processes* are effortful operations that include retrieving contextual details and using them to infer the order of past events (Curran & Friedman, 2003; Skowronski, Walker, & Betz, 2003). For example, when trying to determine if, during a 1-day tour of Paris, the visit to the Louvre occurred before or after lunch, one might remember the pleasant feeling of resting tired legs in a comfortable restaurant chair and conclude that the visit to the Louvre happened before lunch. Moreover, this inference might be confirmed by the image of walking from the Louvre to a nearby restaurant in the Rue de Rivoli. In contrast, *distance processes* are less effortful operations that rely on feelings associated with the strength of the memory trace. For example, one does not need to use reconstruction processes to conclude that the clearly remembered trip to Paris occurred more recently than a vaguely remembered trip to London. Although reconstruction and distance processes could be used to discern the temporal order of the same set of events, reconstruction processes are generally more effective for events that are relatively close in time, whereas distance

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processes are usually more effective for events that are sufficiently far away (Burt, Kemp, Grady, & Conway, 2000; for reviews see Friedman, 1993, 2004). Closeness in time benefits reconstruction processes because it makes causal links more obvious. In the aforementioned example, reconstructing the Louvre–restaurant order is facilitated by the causal relationship between walking and feeling tired, which might not exist if these events occurred farther away in time. In contrast, closeness in time reduces the effectiveness of distance processes because it attenuates differences in memory strength. It is worth noting that distance processes might be used for ordering events that are close in time when the interval between encoding and retrieval is very short, as is the typical case in laboratory studies of temporal-order memory (e.g., comparing the order of words presented 2 min ago vs. 5 min ago in the same list). In contrast, the use of sensory-poor, causally unrelated stimuli in these studies hinders the use of reconstruction processes (e.g., it is difficult to reconstruct what happened between the two words).

In sum, temporal-order memory for autobiographical events is likely to involve both reconstruction processes (increase with closeness) and distance processes (decrease with closeness); in contrast, temporal-order memory for laboratory events often taps mainly distance processes. Thus, although several functional neuroimaging studies have investigated temporal-order memory for laboratory events (Konishi, Asari, Jimura, Chikazoe, & Miyashita, 2006; Konishi et al., 2002; Suzuki et al., 2002; Cabeza et al., 1997; Eyler Zorilla et al., 1996; Nyberg et al., 1996), it is critical to also investigate the neural correlates of temporal-order memory for more complex real-world events, such as autobiographical memories.

The reconstruction–distance distinction (Friedman, 1993, 2004) in retrieving temporal-order memory for autobiographical events is similar to the recollection–familiarity distinction (Yonelinas, 2002; Mandler, 1980) in memory retrieval (see also Bastin, Van der Linden, Michel, & Friedman, 2004; Curran & Friedman, 2003). Like recollection, reconstruction involves the recovery of contextual details, and, similar to familiarity, distance processes rely on the strength of memory traces. There is growing evidence that recollection and familiarity involve distinct neural correlates (Eichenbaum, Yonelinas, & Ranganath, 2007; Rugg & Yonelinas, 2003). Recollection is associated with greater activity in regions including the left PFC (Dobbins, Simons, & Schacter, 2004; Dobbins, Rice, Wagner, & Schacter, 2003; Eldridge, Knowlton, Furmanski, Bookheimer, & Engel, 2000; Henson, Rugg, Shallice, Josephs, & Dolan, 1999), hippocampus and posterior parahippocampal cortices (Eldridge et al., 2000; for a review, see Eichenbaum et al., 2007), posterior cingulate/precuneus cortices (for a review, see Wagner, Shannon, Kahn, & Buckner, 2005), and the visual cortex (Cabeza et al., 2004; Kahn, Davachi, & Wagner, 2004; Wheeler, Petersen, & Buckner, 2000).

In contrast, familiarity processes have been associated with greater activity in regions such as the right PFC (Dobbins et al., 2003, 2004; Henson, Rugg, et al., 1999) and perirhinal cortices (for a review, see Eichenbaum et al., 2007). In sum, recollection and familiarity processes differ with respect to activation in the MTL and posterior brain regions and hemispheric asymmetry in PFC. Previous fMRI studies have also associated differences in PFC lateralization with retrieval success (hits > misses) and retrieval effort (misses > hits). We and others have associated the left PFC with retrieval success (Prince, Daselaar, & Cabeza, 2005) and the right PFC with retrieval effort (e.g., Fleck, Daselaar, Dobbins, & Cabeza, 2006; Henson, Rugg, Shallice, & Dolan, 2000), and others have found hemispheric asymmetries in PFC activity that reflect qualitative rather than quantitative differences (Dobbins et al., 2003; Dobbins, Foley, Schacter, & Wagner, 2002; Ranganath, Johnson, & D'Esposito, 2000). For example, in an event-related fMRI study, Dobbins et al. (2003) found that source-memory judgments activated the left more than the right PFC, whereas recency judgments activated the right more than the left PFC, but importantly, lateralization differences were independent of retrieval success. Thus, accuracy might also be an important factor in distinguishing the neural correlates of the reconstruction–distance distinction.

Although some fMRI evidence is available regarding the contribution of these regions in temporal-order memory for laboratory stimuli (Konishi et al., 2002, 2006; Suzuki et al., 2002), their contribution to temporal-order memory for autobiographical stimuli is unknown. The goal of the present study was to investigate the neural correlates underlying temporal-order memory for autobiographical events. To address this goal while maintaining control over critical memory factors, such as accuracy, we adapted a novel photo-paradigm we previously applied to recognition memory of autobiographical versus laboratory events (Cabeza et al., 2004) in order to investigate memory for temporal order. In our previous study (Cabeza et al., 2004), we found that memories elicited via the photo-paradigm contained greater self-referential processing, visual/spatial imagery, and recollection compared to laboratory memories, therefore validating the use of this paradigm to study the retrieval of complex real-life events or controlled autobiographical memories (for a review, see Cabeza & St. Jacques, 2007).

Given that reconstruction processes are more effective for discriminating events close in time, whereas distance processes are more effective for discriminating events farther away in time, we assumed that brain regions involved in reconstruction processes would show greater activity for shorter than longer lags, whereas regions involved in distance processes would show greater activity for longer than shorter lags (e.g., Suzuki et al., 2002). Our fMRI predictions were based on the similarity between the reconstruction–distance distinction (Friedman, 1993, 2004) and the recollection–familiarity

distinction (Yonelinas, 2002; Mandler, 1980). We predicted that reconstruction processes during shorter lags would involve regions previously associated with recollection, such as the left PFC, hippocampus and posterior parahippocampal cortices, posterior cingulate/precuneus cortices, and the visual cortex. In contrast, distance processes during longer lags would involve regions previously associated with familiarity, such as the right PFC and perirhinal cortices. In sum, we predicted that temporal-order decisions for shorter lags (reconstruction processes/recollection) would differentially engage the left PFC and temporal-order decisions for longer lags (distance processes/familiarity) would differentially engage the right PFC. On the basis of Dobbins et al.'s (2003) findings, we predicted that this hemispheric asymmetry would not vary with retrieval success (hits vs. misses). Additionally, we predicted that shorter lags would elicit greater activity in other regions associated with recollection, such as the hippocampus and posterior parahippocampal cortices, posterior cingulate/precuneus cortices, and the visual cortex.

METHODS

Participants

Seventeen young adults (9 men; mean age = 21.6, SD = 2.7) participated in the study. Participants were healthy, right-handed, native English speakers, with no history of neurological or psychiatric episodes. They were mostly undergraduate students at Duke University and, in all cases, were very familiar with the Duke campus. Participants gave written informed consent for a protocol approved by the Duke University Institutional Review Board.

Materials and Procedure

Photo-taking Session

The study took place on two consecutive days. On Day 1, participants took 480 photographs at 80 campus locations (6 pictures per location). The locations were well-known places within the Duke West Campus (e.g., the Duke Chapel), both indoors and outdoors. The order of the locations was selected to reduce the correlation between temporal distance and spatial distance, r = .13, p = .07, such that participants visited new locations in the same building/spatial region at different time points during the day and followed a circular route in that they started and ended at the same building (for examples, see Figure 1A). Participants were provided with a digital camera (Kodak Easy Share CX6200), a booklet with 80 locations (one per page), and training on how to use the camera and take photos. Participants were provided with instructions during the encoding task. They were told that the study was interested in how people take photographs and they were asked to consider each photo as a distinct event by paying attention to the particular physical (e.g., viewpoint, body position, etc.) and psychological (e.g., preference, mood, etc.) phenomena associated with each picture to ensure that they were not simply clicking the camera without viewing the scene they were photographing. The photo-taking session was a classic incidental encoding task, with instructions designed to draw attention from intentional memory encoding and with no mention of a subsequent memory test. Participants were instructed to complete the photo-taking task without stopping for breaks so that picture taking was continuous (mean time = 5.00 hr, SD = 0.40 hr). The camera's LCD screen was blocked to prevent participants from reviewing the photos. At each location, participants took six pictures from different positions and/or angles. Participants were instructed to tear off one page of the booklet after each location so that at the end of the photo session the whole booklet would be completed. The cameras were returned to the lab immediately after the last picture was taken, and the photographs were digitally enhanced using a finite impulse response (FIR) filter.

Scanned Task

On Day 2, participants were scanned using an event-related fMRI design while making temporal-order judgments on their photographs from the previous day. Across 5 scans of 30 trials each, they were shown 180 photograph pairs from different locations (2 photos side by side) and were asked to indicate which picture they took first and whether the decision was made with low or high confidence (i.e., definitely left, probably left, probably right, definitely right). We manipulated the lag between pairs of photos from short (1 to 9 locations apart), medium (10 to 39 locations apart), and long (40 to 80 locations apart) so that lags were equally spaced on a logarithmic scale. Photo pairs were selected so that the campus locations were equally represented across time lag. Each photo was presented for 4 sec, followed by a self-paced response screen (up to 6 sec), and then by a fixation cross for a varying interval between 500 and 2500 msec plus any additional time from the response screen (total trial length = 10.50 to 12.50 sec; see Figure 1B). Reaction times were not informative because participants were required to wait until the response screen appeared before making a response. The rationale for this procedure was to allow for equal viewing time in each condition. Postscanning, participants were asked rate their familiarity with each of the 80 campus locations (1 = low to 4 = high). Debriefing suggested that participants were unaware of the nature of the scanning task during the photo-taking session.

fMRI Methods

Scanning

Scanning was conducted using a 4-T GE magnet. Stimuli were presented using liquid crystal display goggles
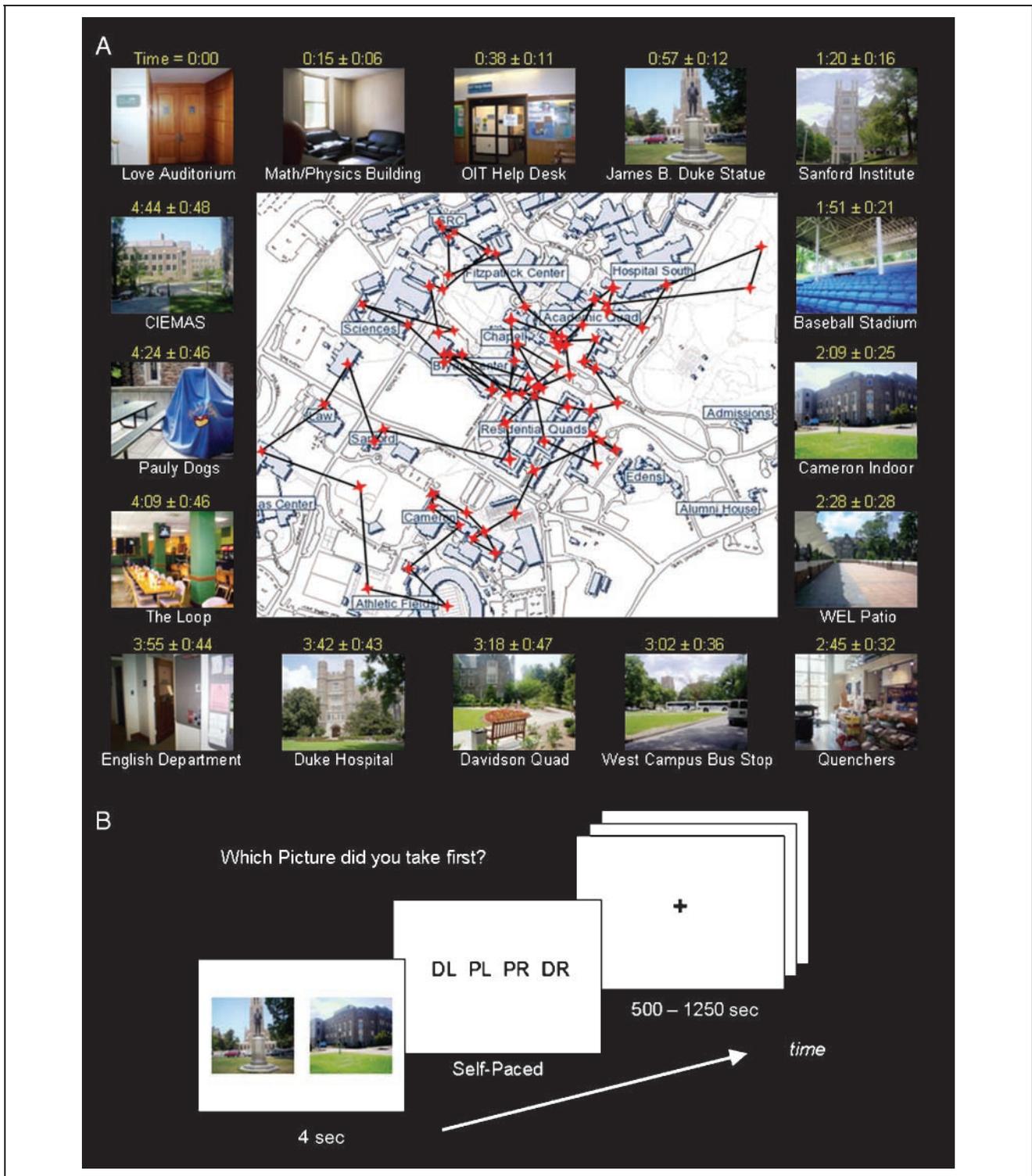
Figure 1. (A) The Duke campus map shows the locations and route of the locations where the photographs were taken prior to scanning. Examples of photographs taken by participants with the average time (in hours and minutes) and the *SD* to visit the locations are depicted. (B) During scanning, participants saw pairs of photographs taken on the previous day and were asked to make temporal-order judgments and whether the decision was made with low or high confidence. DL = definitely left; PL = probably left; PR = probably right; DR = definitely right.

(Resonance Technology, Northridge, CA) and behavioral responses were recorded using a four-button fiber-optic response box (Resonance Technology). Head motion was minimized using foam pads and a headband. Ana-

tomical scanning started with a T1-weighted sagittal localizer series. The anterior (AC) and posterior com-missures (PC) were identified in the midsagittal slice, and 34 contiguous oblique slices were prescribed parallel to

the AC–PC plane. High-resolution T1-weighted structural images were acquired with a 12-msec repetition time (TR), a 5-msec echo time (TE), 24 cm field of view (FOV), 68 slices, 1.9 mm slice thickness, and a 256^2 matrix. Functional scanning employed an inverse spiral sequence with a 1500-msec TR, 36 msec TE, 24 cm FOV, a 64^2 image matrix, and a 60° flip angle. Thirty-four contiguous slices were acquired with the same slice prescription as the anatomical images. Slice thickness was 3.75 mm, resulting in 3.75 mm^3 isotropic voxels.

fMRI Analyses

Image processing and analyses were performed using Statistical Parameter Mapping software implemented in Matlab (SPM2; Wellcome Department of Cognitive Neurology, London, UK). Functional images were corrected for slice acquisition order, realigned to correct for motion artifacts, and then spatially normalized to a standard stereotactic space, using the template implemented in SPM2. Subsequently, the functional images were spatially smoothed using an 8-mm isotropic Gaussian kernel. For each subject, evoked hemodynamic responses to event types were modeled with a delta (stick) function corresponding to 2 sec after stimulus presentation (the middle of the photograph presentation time), convolved with a canonical hemodynamic response function within the context of the General Linear Model (GLM). This onset was selected because behavioral pilot data suggested that it took participants a couple of seconds to identify the locations, and we were primarily interested in the decision process.

Short vs. Long Contrast

To isolate activity in the brain that was exclusively involved in the short and long time lag conditions, we employed the GLM to generate contrasts for the temporal-order memory for correct trials with each of the time lag conditions, as well as, the short versus long contrast. Subsequently, random-effects analysis was performed on the parameter estimates of the conditions ($p = .05$, uncorrected, with a cluster size > 15 voxels). We used a cluster-size threshold ($R = 15$) to establish a Type 1 error level of $p < .005$ for false discovery of voxels within each cluster (Forman et al., 1995). In order to isolate activity exclusive to short versus long conditions, we inclusively masked this contrast with the effect of the time lag condition of interest (short or long) greater than baseline fixations at $p = .001$. Thus, the resulting activity isolating activity related to short or long conditions also had to be confirmed by real differences observed in each time lag condition in comparison with the implicit baseline (short > baseline, long > baseline).

Parametric Contrasts

To examine changes in the neural correlates modulated by temporal distance, we employed a parametric approach, which allowed us to examine how activity was modulated as a function of discrete changes in time lag as opposed to examining only the overall activity level averaged within the short and long time lag bins. To identify ROIs showing temporal-order memory-related activity increases as a function of increasing lag, we created a GLM in which correct trial onsets were modulated by the lag between pairs of photographs (e.g., from lags of 1 to 80) using the first-order parametric modulation option integrated in SPM2 and its reverse (i.e., increasing activity associated with decreasing time lag). The pairs of photographs also differed with respect to spatial distance and we entered this factor as a covariate in the model. Thus, we examined the unique contribution of temporal lag orthogonalized with respect to spatial distance in the design matrix. Confidence responses were combined because they did not produce any additional information. Subsequently, random-effects analyses were performed on the parameter estimates of the parametric regressor for temporal lag and spatial distance ($p = .05$, uncorrected, with a cluster size > 15 voxels). We used a cluster-size threshold ($R = 15$) to establish a Type 1 error level of $p < .005$ for false discovery of voxels within each cluster (Forman et al., 1995). In order to examine positive activations in each of the conditions of interest, we inclusively masked with a contrast of the main effect of correct trials greater than baseline fixations at $p = .001$. Additionally, to examine activity in the temporal lag condition that did not overlap with activity in the spatial distance condition, we employed an additional exclusive mask at $p = .001$. We did not further examine spatial distance because it was not the main focus of the study (i.e., participants were only asked to make a temporal-order decision and the circular path during the photo-taking session was not appropriate for this goal).

Accuracy and Difficulty

Regions identified by the parametric modulation of time lag, which were greater than baseline, were further interrogated to determine if there were effects of accuracy (hits > misses). To create these contrasts, we employed the GLM to generate parameter estimates for hit and miss responses in a separate design matrix. Statistical parametric maps were created for each subject by applying linear contrasts to the parameter estimates for these events of interest, resulting in a t statistic for every voxel. We performed additional random-effects analyses to determine the effects of retrieval accuracy. A liberal threshold was chosen in order to maximize the power to detect the effects of accuracy in regions demonstrating parametric modulation (both at $p = .05$, uncorrected,

with cluster size > 5). Because we were only interested in changes in the neural correlates of temporal-order memory, we used the results from the parametric modulation and its reverse as spatial inclusive masks for the contrasts of retrieval accuracy. Thus, we defined masks in which activity had to be above baseline fixation, which demonstrate a parametric modulation by temporal lag and show changes as a function of accuracy. Finally, we examined the effects of task difficulty and familiarity by entering each participant's overall accuracy and familiarity scores as a covariate in the parametric analysis on temporal lag.

RESULTS

Behavioral Results

As expected, there was a significant difference in accuracy (proportion correct) as a function of lag [$F(2, 16) = 24.05, p < .0001$; see Figure 2]. Shorter lags ($M = 0.74$, $SD = 0.07$) were less accurate than medium lags ($M = .82, SD = .07$) [$t(16) = 4.49, p < .0005$] and longer time lags ($M = 0.87, SD = 0.06$) [$t(16) = 6.42, p < .0001$], which also differed from one another [$t(16) = 2.85, p < .05$]. The overall familiarity scores suggested that participants were generally familiar with the campus ($M = 3.08, SD = 0.51$).

fMRI Results

Table 1 lists regions revealed in the direct contrast of the short versus long time lag conditions. Consistent with our predictions, the left dorsolateral PFC showed greater activity for the short lag condition, whereas the right dorsolateral PFC showed greater activity for the long time lag condition. Given that left versus right PFC regions have been respectively associated with recollection and familiarity (Dobbins et al., 2003; Henson, Rugg, et al., 1999), this hemispheric asymmetry finding
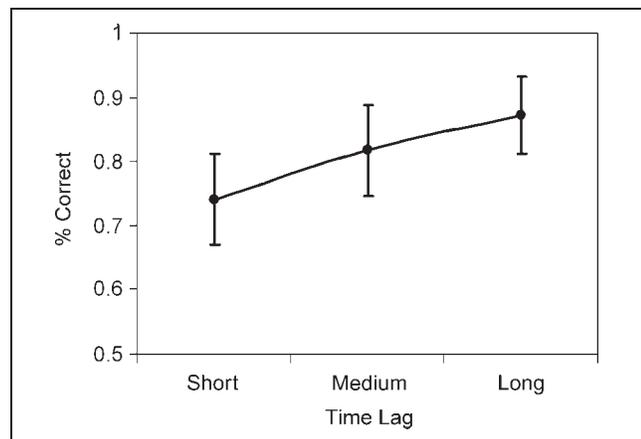
Figure 2. Mean proportion correct for short, medium, and long time lags. Error bars indicate standard error of the mean.

supports our hypothesis that reconstruction processes depend on recollection, whereas distance processes depend on familiarity. Also consistent with our hypotheses, the short time lag condition elicited greater activity in other regions associated with recollection, including the MTL (right parahippocampal gyrus), the posterior midline cortex (retrosplenial, posterior cingulate, precuneus), and the visual cortex/cuneus, extrastriate including bilateral activity in the precuneus, posterior cingulate, and cuneus. Although the long time lag condition did not show activity in the perirhinal cortex, we also found activity in the right fusiform gyrus, angular gyrus, and superior parietal cortex.

Furthermore, we also identified regions where activity monotonically increased or decreased as a function of time lag using parametric modulation analyses on the fMRI activity that were mutually exclusive from the effects of spatial distance (see Table 2 and Figure 3). In these parametric analyses, lag was entered as a continuous variable (lag 1 to 80) but, for display purposes, the line graphs in Figure 3 show that fMRI activity averaged across three lag ranges: short (lag 1 to 9), medium (lag 10 to 39), and long (lag 40 to 80). Likewise, to simplify the description of results, activity that parametrically decreased or increased as a function of lag is respectively described as "greater for shorter lags" or "greater for longer lags."

As indicated by Table 2 and Figure 3, a subset of the regions found in the direct contrast also showed activity that monotonically increased or decreased as a function of time lag, and are consistent with our predictions. We found hemispheric asymmetry in PFC, with greater activity in the left dorsolateral PFC for shorter lags, whereas the right dorsolateral PFC showed greater activity for longer lags. Shorter lags also elicited greater activity in other regions associated with recollection, including the MTL (right parahippocampal gyrus), the posterior midline cortex (retrosplenial, posterior cingulate, precuneus), and the visual cortex/cuneus, extrastriate including bilateral activity in the precuneus, posterior cingulate, and cuneus. In contrast, longer lags revealed greater activity in the right fusiform gyrus. Because of our a priori hypothesis about the hippocampus and perirhinal cortices, we further examined activity in the MTL using a less conservative threshold ($p = .05$, with a cluster size > 5 voxels and inclusively masked with the main effect of temporal-order trials greater than baseline fixations at $p = .05$). Shorter lags revealed greater activity in the left hippocampus, whereas longer lags did not reveal any activity in the MTL. Thus, the results of the parametric analysis support the prediction that the neural correlates of temporal-order memory decisions differ according to shorter and longer time lags, irrespective of how "short" or "long" conditions are categorized.

To confirm the hemispheric asymmetry in the dorsolateral PFC, we extracted the peak responses in each hemisphere and entered these into a Hemisphere (left,

Table 1. Brain Regions Showing Activity in Short versus Long Time Lags

| Region | BA | H | Talairach Coordinates | | | Voxels | t Score |
			x	y	z		
Long > Short							
Dorsolateral PFC	9	R	48	8	24	30	2.70
Premotor cortex	6	L	−41	6	49	15	3.05
Superior parietal	7	R	26	−53	41	27	2.55
Angular gyrus	39	R	52	−69	14	19	3.43
Fusiform gyrus	37	R	37	−44	−14	91	3.16
Short > Long							
Dorsolateral PFC	46	L	−41	26	20	49	2.93
Premotor cortex	6	L	−30	6	56	23	3.36
Central cingulate gyrus	32	L	−4	17	45	43	3.99
Parahippocampus		R	19	−37	−5	60	3.46
Posterior cingulate	31	L	−7	−65	21	224	3.75
		R	11	−57	20	224	3.50
Retrosplenial cortex	30	L	−7	−51	6	224	2.85
Precuneus	7	R	7	−63	52	15	3.24
Visual cortex/cuneus	17/18	L	−15	−99	−5	91	4.60
		R	15	−98	−1	75	2.94
	19	L	−37	−78	35	43	4.08

BA = Brodmann's area; H = hemisphere.

All ps < .005.

right) × Time lag (short, long) repeated ANOVA (only two levels of time lag were used because we were interested in examining the extremes). This analysis yielded significant two-way interaction [$F(1, 16) = 32.23, p < .0001$] and follow-up tests revealed that activity was greater for shorter than longer lags in the left dorsolateral PFC [$t(16) = 3.13, p < .01$], whereas the opposite was true in the right dorsolateral PFC [$t(16) = 2.70, p < .05$].

To investigate the relationship between the hemispheric asymmetry in PFC activity and potential differences in retrieval success and task difficulty, we conducted two ancillary analyses on the regions that showed time lag effects. First, we determined whether activity in these regions differed between hits and misses. As illustrated by Figure 4, no significant differences between hits and misses were found either in the left or right PFC (main effect of item: $p = .12$; Item × Hemisphere interaction: $p = .36$), nor in other brain regions. Second, we determined whether activity in the regions showing an effect of time lag varied as a function of task difficulty by entering accuracy as a covariate and there was no affect on the parametric analyses. Finally, the main findings from the

parametric analysis were not affected by entering familiarity as a covariate.

DISCUSSION

The results of the present study suggest that reconstruction and distance are distinct processes involved in temporal-order memory for autobiographical events, and that these processes are differentially recruited depending upon the temporal distance between events. The study yielded three main findings. First, when events occurred closer in time, activity in the left dorsolateral PFC, the MTL, as well as the left parietal, posterior midline, and visual cortices, indicated that temporal-order memory involved the recollection of contextual details. Second, when events occurred further away in time, activity in the right dorsolateral PFC and the fusiform gyrus indicated that temporal-order memory involved familiarity processes. Finally, the left lateralization of PFC activity for shorter lags, coupled with the right lateralization of PFC activity during longer

Table 2. Brain Regions Showing Activity Parametrically Modulated by Time Lag

Region	BA	H	Talairach Coordinates x	y	z	Voxels	t Score
Longer Time Lags							
Dorsolateral PFC	9	R	48	8	24	16	3.35
Fusiform gyrus	37	R	48	−52	−13	65	2.84
Shorter Time Lags							
Dorsolateral PFC	46	L	−41	23	20	51	2.66
Central cingulate gyrus	32	L	−4	17	45	61	3.95
Parahippocampus		R	19	−37	−5	–	3.42
Posterior cingulate	31	L	−15	−61	21	123	4.28
	31	R	11	−57	20	–	3.63
Retrosplenial cortex	30	L	−11	−54	6	–	3.75
	29/30	R	11	−51	10	–	3.81
Precuneus	7	L	−30	−45	41	30	2.62*
Visual cortex/cuneus	17/18/19	L	−15	−99	−5	136	4.58
	18	R	19	−98	−1	298	2.75
	19	L	−37	−79	32	59	4.05
		R	41	−75	35	17	3.27

BA = Brodmann's area; H = hemisphere.

All *p*s < .005, unless otherwise indicated.

*p < .01.

lags, yielded a marked hemispheric asymmetry in PFC activity. We discuss these three findings in separate sections below.

Regions Associated with Reconstruction Processes during Shorter Time Lags

At shorter time lags, a network of brain regions was activated, including the left dorsolateral PFC and posterior parahippocampal, parietal and visual cortices, suggesting that recollection of contextual details was utilized to temporally parse the events. Several studies have indicated a greater role for the left PFC during tasks involving recollection (Kahn et al., 2004; Dobbins et al., 2002, 2003; Ranganath et al., 2000; Raye, Johnson, Mitchell, Nolde, & D'Esposito, 2000; Henson, Rugg, et al., 1999; Rugg, Fletcher, Chua, & Dolan, 1999; Nolde, Johnson, & D'Esposito, 1998), with the majority of studies reporting activity in the dorsolateral PFC as in the present study (for exceptions, see Kahn et al., 2004; Rugg et al., 1999). The left dorsolateral PFC involvement in recollection memory is thought to reflect an increase in reflective and evaluative demands, and greater episodic specificity during the retrieval of contextual infor-

mation. The left dorsolateral PFC has also been found in laboratory memory studies that have specifically investigated temporal context memory (Konishi et al., 2002; Suzuki et al., 2002; Cabeza et al., 1997). For example, Suzuki et al. (2002) manipulated the temporal distance between pairs of line drawings by as much as 3 hr, which is more similar to the present time frame. Consistent with the results of the present study, Suzuki et al. found greater left dorsolateral PFC activity for temporal judgments made for pairs of drawings separated by shorter temporal distances than those separated by longer distances. The results of the present study allow us to further characterize the involvement of the left dorsolateral PFC in temporal memory for autobiographical events involving a richer and extensive temporal context.

As predicted, we found greater activity in the posterior parahippocampus for shorter lags, but the hippocampus activity was subthreshold. These results suggest that although the hippocampus was recruited, suggesting that the photo-paradigm was eliciting recollection of autobiographical events (e.g., Cabeza et al., 2004), activity in this region did not differentiate the temporal-order effects as strongly as the posterior parahippocampus.
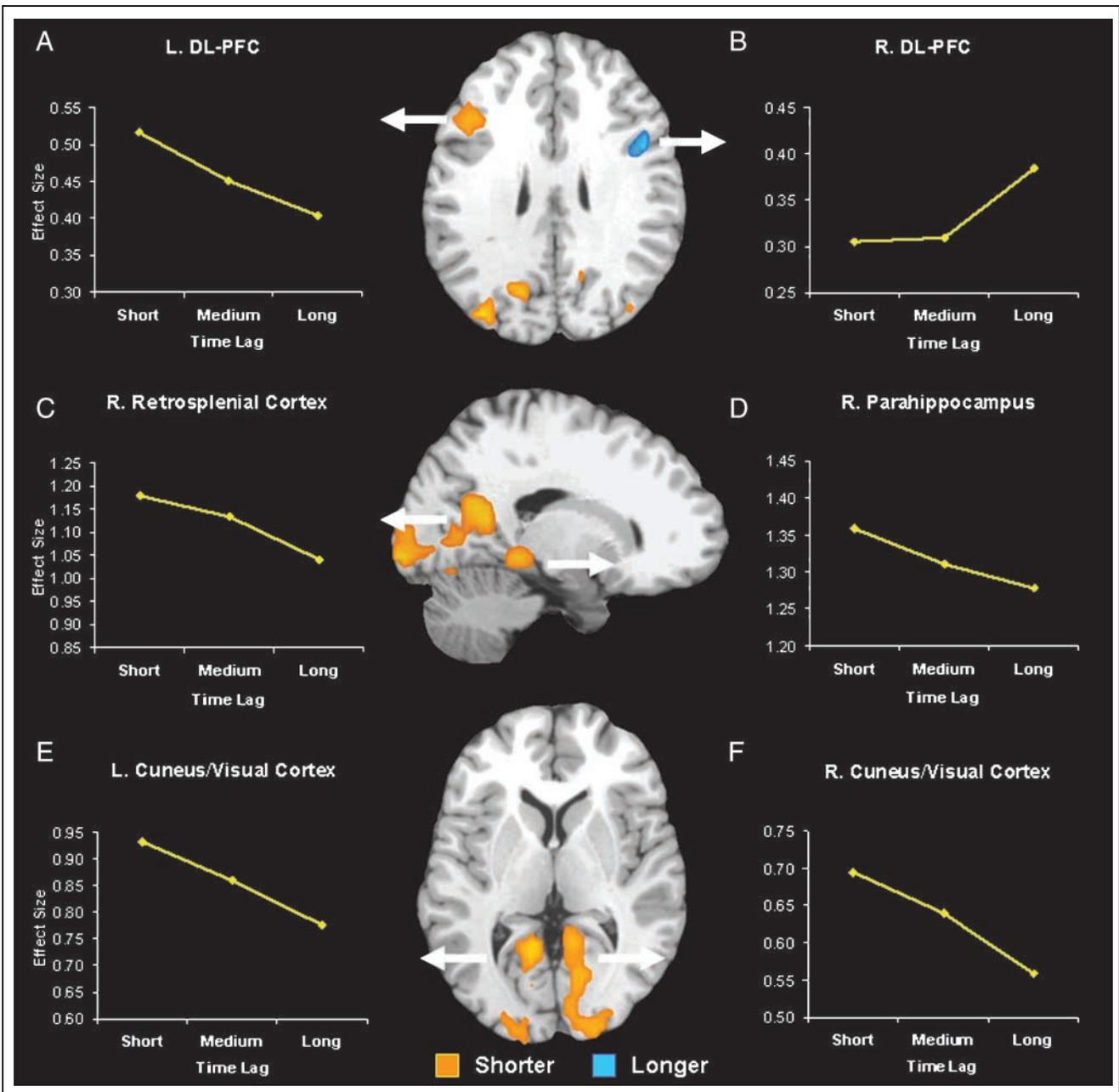
Figure 3. Activity parametrically modulated by increasing time lag (longer) and decreasing time lag (shorter), which was mutually exclusive from spatial distance.

The finding that the right posterior parahippocampal cortex was associated with reconstruction of temporal context is consistent with three different accounts of parahippocampal function. First, several fMRI studies, including studies using words and objects, have associated the posterior parahippocampal gyrus with recollection and relational memory (e.g., Wais, Wixted, Hopkins, & Squire, 2006; Prince et al., 2005; Yonelinas, Otten, Shaw, & Rugg, 2005; Kahn et al., 2004; Yonelinas, Hopfinger, Buonocore, Kroll, & Baynes, 2001; Eldridge et al., 2000). In the present study, the parahippocampal activation could have reflected the recollection of the

photo-taking episodes, which is required to reconstruct the order of events close in time. Second, the posterior parahippocampal gyrus has been strongly associated with spatial scene perception. In particular, a region dubbed the ''parahippocampal place area'' has been found to be more activated during the processing of spatial layout than during the processing of objects, faces, and other control stimuli (Epstein & Kanwisher, 1998). The reported parahippocampal activation was near the putative parahippocampal place area and might have reflected the processing of the spatial aspects of retrieved mental images or the photos used

Figure 4. Activity related to hits and misses in the left and right dorsolateral PFC for shorter and longer time lags, respectively.
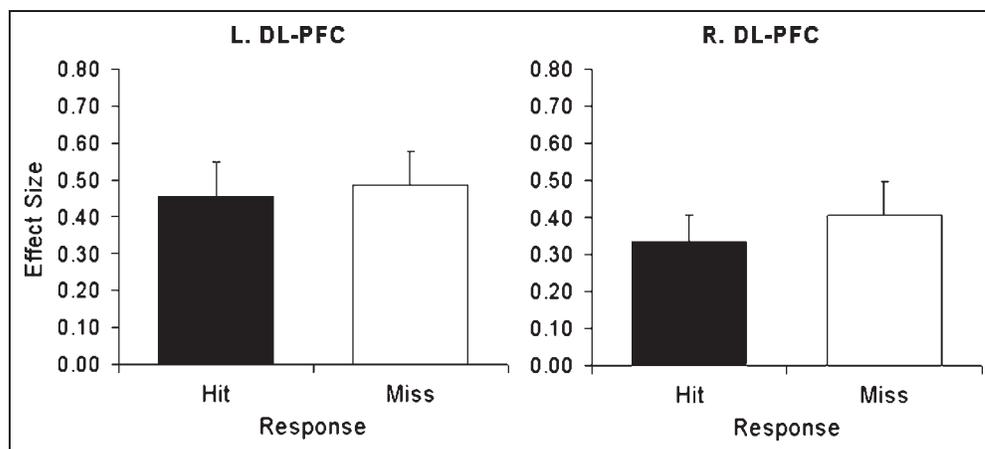
as cues. However, it is not clear why spatial scene processing would differ as a function of decreasing temporal distance. Third, the parahippocampus has been linked to mental navigation and retrieval of topographical information (e.g., Mellet et al., 2000; Aguirre, Zarahn, & D'Esposito, 1998; Maguire, Burgess, et al., 1998; Maguire, Frith, Burgess, Donnett, & O'Keefe, 1998; for a review, see Burgess, Maguire, & O'Keefe, 2002), which might be more important as spatial distance decreases. However, in the present study, temporal distance was not significantly positively correlated with spatial distance. Furthermore, the reported activity in the parametric analysis on temporal lag did not overlap with activity reflecting spatial distance. Thus, of these accounts, the involvement of the posterior parahippocampus in recollection is the most parsimonious within the framework of the present study, in which both spatial and other information linked to the photo-taking event might contribute to reconstructing the temporal-order memory. Future work is needed to clarify the role of the MTL, including the involvement of the hippocampus, in temporal-order memory for autobiographical events relying on reconstructive processes.

In addition to PFC and MTL regions, recollection for temporal judgments involving shorter time lags also engaged intervening posterior parietal, posterior midline (retrosplenial, posterior cingulate, precuneus), and visual cortex regions. Posterior parietal and posterior midline activations are among the most typical findings in functional neuroimaging studies of episodic memory retrieval (for a review, see Cabeza & Nyberg, 2000). Several fMRI studies have linked subregions of parietal and posterior midline cortices with recollection (for a review, see Wagner et al., 2005). For example, we recently found recollection-related activity in left parieto-temporal and retrosplenial regions very close to the ones we observed here (Daselaar, Fleck, & Cabeza, 2006). Damage to the retrosplenial cortex can cause amnesia (Valenstein et al., 1987), and in the right side it has been found to specifically affect memory for spatial relationships (for a re-

view, see Maguire, 2001). Thus, in our study, this region might contribute to both recollection and spatial memory. As for the precuneus, some evidence has linked its role in memory retrieval to the processing of visual images (Fletcher et al., 1995), and this function might have contributed to the reconstruction of temporal order. Finally, activations in the visual cortex and cuneus regions likely reflect the retrieval of visual details (for a review, see Buckner & Wheeler, 2001), which is critical for autobiographical memory retrieval (Daselaar et al., 2008; Greenberg, Eacott, Brechin, & Rubin, 2005; Rubin, Burt, & Fifield, 2003; Rubin & Greenberg, 1998). In a prior study using the photo-paradigm (Cabeza et al., 2004), we found greater visual cortex and cuneus activity when participants recognized campus photos they took themselves compared to similar photos taken by others.

Regions Associated with Distance Processes during Longer Time Lags

The analysis identifying brain regions where activity increased as a function of lag yielded only two regions: the right dorsolateral PFC and right fusiform areas. The finding of right dorsolateral PFC activity in association with long lags is consistent with functional neuroimaging evidence linking this region to familiarity (Dobbins et al., 2004; Eldridge et al., 2000; Henson, Rugg, et al., 1999). A related interpretation of these right PFC activations is that they reflect an increase in monitoring for items that are close to the response criterion (Henson et al., 2000). This issue is discussed in the next section. The present right dorsolateral PFC activation is also consistent with several studies investigating temporal context memory that have reported activations in this region (Fujii et al., 2004; Dobbins et al., 2003; Konishi et al., 2002; Suzuki et al., 2002; Cabeza et al., 1997). Some of these studies also found activations in the left PFC (e.g., Konishi et al., 2002; Cabeza et al., 1997), but these activations might reflect the contributions of recollection to temporal-order judgments in some con-

ditions. In fact, when these contributions are controlled by subtracting out activity during source memory from activity during temporal-order judgments, as done by Dobbins et al. (2003), the resulting pattern of PFC activity is strongly right lateralized.

Turning to the right fusiform gyrus, this is a region that some studies have associated with the processing of specific perceptual information, as opposed with the left fusiform activity, which is assumed to mediate more conceptual or abstract processing (Garoff, Slotnick, & Schacter, 2005; Simons, Koutstaal, Prince, Wagner, & Schacter, 2003; Koutstaal et al., 2001). For example, in one fMRI study (Koutstaal et al., 2001), priming-related activity in the right fusiform gyrus (but not in the left fusiform) was reduced when the perceptual properties of the items changed between study (e.g., a yellow umbrella) and test (e.g., a striped umbrella). In another fMRI study (Garoff et al., 2005), encoding activity in the right fusiform gyrus (but not in the left fusiform) predicted memory for specific perceptual properties of stimuli. Thus, the right fusiform gyrus seems to be involved in processing item-specific perceptual information, which might underlie familiarity processes (Whittlesea & Williams, 2000; Jacoby & Dallas, 1981; Mandler, 1980; although see Voss & Paller, 2006). The role of the right fusiform gyrus in temporal-order decisions for longer lags might reflect greater reliance on perceptual aspects of the information during distance judgments. For instance, participants could have ordered the two photos in time by paying attention to their perceptual details. Although we predicted greater activity for longer lags in the perirhinal cortex, a region important for familiarity processes (e.g., Eichenbaum et al., 2007), the results of the present study suggest instead that perceptual fluency via the fusiform gyrus is involved in temporal-order memory judgments for autobiographical events separated by longer time lags and that activity in this region might underlie distance processes. Further work is needed to clarify the role of the perirhinal cortex and other regions that might mediate distance processes.

Hemispheric Asymmetry in PFC Activity

The main finding of the present study was a hemispheric asymmetry in the dorsolateral PFC during temporal-order memory such that the left PFC showed greater activity for shorter than longer time lags and the right PFC showed greater activity for longer than shorter lags. The hemispheric asymmetry we observed is consistent with our hypothesis that reconstruction versus distance processes are similar to recollection versus familiarity processes, respectively, which have been previously associated with left versus right PFC activations (Dobbins et al., 2003, 2004; Eldridge et al., 2000; Henson, Rugg, et al., 1999). For example, Henson, Rugg, et al. (1999) used the ''remember–know'' procedure (Tulving, 1985) to determine when memory is accompanied by contex-

tual details (''remember'' judgment) versus when it is not (''know'' judgment), as based on participant introspections. The study yielded greater left dorsolateral PFC activity for remember responses (recollection), but greater right dorsolateral PFC activity for know responses (familiarity). Thus, the hemispheric asymmetry in the present study extends this finding to the temporal-order memory domain, supporting the hypothesis that temporal-order decisions for shorter versus longer lags are based on reconstruction (recollection) versus distance (familiarity) processes, respectively.

Importantly, the hemispheric asymmetry in PFC activity cannot be attributed to differences in retrieval success. Although PFC activity varied as a function of time lag, it did not differ as a function of accuracy; in both the left and right dorsolateral PFC, activity was similar for hits and misses (see Figure 4). This finding is consistent with several fMRI studies showing that during episodic retrieval some PFC regions are sensitive to retrieval orientation rather than to retrieval success (Kahn et al., 2004; Dobbins et al., 2002, 2003; Ranganath et al., 2000; for a review, see Rugg & Wilding, 2000). For example, in Dobbins et al. (2003), recollection-related left PFC activity and familiarity-related left PFC activity did not differ between correct and incorrect memory decisions. The results of the present study are consistent with retrieval orientation accounts of PFC function, whereby activity reflects the processes involved during the attempt to retrieve irrespective of retrieval success. Moreover, including accuracy as a covariate did not affect the results of the parametric analysis, which further supports the suggestion that activity in these regions is independent of retrieval effort and task difficulty.

Beyond the recollection–familiarity distinction, another account that explains the hemispheric asymmetry finding is the distinction between systematic and heuristic processes (Nolde, Johnson, & Raye, 1998). *Systematic processes* involve the retrieval of more detailed information that engages greater reflection and evaluation, such as during source-memory attributions, and relies on the left PFC. In contrast, *heuristic processes* involve the simple maintenance of information and comparison of that information to a response criterion, such as during simple item-recognition tasks, and relies on the right PFC. Like the recollection–familiarity distinction, the systematic–heuristic distinction is supported by a substantial amount of evidence (Dobbins et al., 2002; Ranganath et al., 2000; Raye et al., 2000; Rugg et al., 1999; Nolde, Johnson, & D'Esposito, 1998; Nolde, Johnson, & Raye, 1998). The present hemispheric asymmetry finding can be easily explained in terms of the systematic–heuristic distinction because making temporal-order decisions for shorter lags requires the systematic evaluation of available source information. Conversely, temporal-order decisions for longer lags can be based on a simple heuristic evaluation of memory strength. The systematic–heuristic distinction has been typically investigated by contrasting different

memory tasks (e.g., source memory vs. item recognition; although see Dobbins & Wagner, 2005; Dobbins et al., 2002), but in the present study, we found differences consistent with this distinction within the same task (shorter vs. longer lags). This result provides further support for the idea that the critical factor determining PFC activity is not the type of task but the type of memory processes recruited by the task. These results are consistent with the source-monitoring framework (Johnson et al., 1993), which proposes that performance in source-memory tasks involves both systematic and heuristic processes (also see Dobbins & Wagner, 2005).

In contrast, our results are less consistent with the postretrieval monitoring account of lateralization differences in PFC activity. Postretrieval monitoring refers to the evaluation of items retrieved from memory in accordance with their accuracy and relevance to the task (Burgess & Shallice, 1996; Koriat & Goldsmith, 1996; Norman & Bobrow, 1979). Evidence from both neuropsychology (Curran, Schacter, Norman, & Galluccio, 1997; Schacter, Curran, Galluccio, Milberg, & Bates, 1996) and neuroimaging (e.g., Allan, Dolan, Fletcher, & Rugg, 2000; Henson et al., 2000; Henson, Shallice, & Dolan, 1999; Rugg et al., 1999) have suggested a role for the right PFC in postretrieval monitoring (also see Fleck et al., 2006). In the present study, we found that activity in the right and left PFC that varied as a function of time lag was not affected by task difficulty. At the same time, the lateralization of PFC varied as a function of recollection versus familiarity (or systematic vs. heuristic) demands, but not as a function of retrieval success, suggesting that retrieval orientation is the critical factor determining PFC lateralization in our task rather than effort or monitoring demands.

Conclusions

In the present study, we employed a novel photo-paradigm to investigate temporal-order memory for autobiographical events, in which we were able to control for the order of when events occurred along with other factors (e.g., Cabeza et al., 2004). Although a controlled way to elicit autobiographical memories, the photo-paradigm replicates the common experience of taking photographs during sightseeing. Unlike typical laboratory stimuli, the use of the photo-paradigm also allowed us to manipulate the temporal distance between events over longer intervals, which was important for separating the processes involved in temporal context memory. Furthermore, in the photo-paradigm, participants were also personally familiar with the campus, and thus, recall of these events might have been influenced by the autobiographical salience associated with particular locations (e.g., Westmacott & Moscovitch, 2003). Although we found that the differences in overall familiarity did not affect the main results, the interaction

between autobiographical significance and temporal context memory will be interesting for future research.

Our results are consistent with behavioral evidence in autobiographical memory, suggesting that there are two distinct processes which are involved in temporal context memory: (1) *reconstruction*, based on the rich recollection of contextual details, and (2) *distance*, based on differences in the familiarity signal (Friedman, 1993, 2004). Reconstruction and distance processes are similar to recollection and familiarity, but not identical. For example, Friedman (1993, 2004) proposed that distance processes are the preferred method for determining temporal context, with reconstruction processes accessed only when accuracy is important (such as in the present study), but not all models of recollection and familiarity make this same assumption (for a review, see Yonelinas, 2002). Although we found parahippocampal activity for shorter lags suggesting the use of reconstruction processes in this condition, activity in the hippocampus was not as strong a predictor of temporal-order memory. Furthermore, although we found activity in the fusiform gyrus for longer lags consistent with the use of distance processes, we did not observe the predicted perirhinal activity. Future research is needed to better characterize how the distance–reconstruction distinction differs from the recollection–familiarity distinction, such as determining the characteristics and content of the autobiographical memories that are retrieved via self-report measures. In particular, the interaction of distance–reconstruction processes and the retrieval of episodic versus semantic autobiographical events (e.g., Cabeza & St. Jacques, 2007; Svoboda, McKinnon, & Levine, 2006), as well as the examination of temporal versus other components of memory (e.g., spatial context; Hayes, Ryan, Schnyer, & Nadel, 2004; Burgess, Maguire, Spiers, & O'Keefe, 2001), are important issues. Despite possible differences between the two constructs, by characterizing these temporal processes within the framework of recollection and familiarity, we were able to make predictions about lateralization differences in PFC and activity in posterior regions, which were not directly discernable in the behavioral model of reconstruction and distance (Friedman, 1993, 2004).

The results of the present study are consistent with prior evidence from lesion and neuroimaging, suggesting that PFC is important for temporal information (e.g., Cabeza et al., 1997; Mangels, 1997; Eyler Zorilla et al., 1996; Nyberg et al., 1996; Butters, Kaszniak, Glisky, Eslinger, & Schacter, 1994; Kesner, Hopkins, & Fineman, 1994; McAndrews & Milner, 1991; Milner et al., 1991; Milner, 1971). However, we extend these findings by showing that the left dorsolateral PFC is particularly implicated in reconstruction-based temporal judgments, whereas the right dorsolateral PFC is involved in distance-based judgments. Furthermore, we found that posterior brain regions were also important in these temporal processes, especially in the case of reconstruction. To our knowledge, this is the first fMRI

study to investigate temporal context memory for autobiographical events. In the present study, the time lag between the events took place within a single day; future studies should probe longer lags between autobiographical events to determine whether the findings generalize to broader temporal distances in memory.

Acknowledgments

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