Common and Unique Neural Activations in Autobiographical, Episodic, and Semantic Retrieval

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Abstract

■ This study sought to explore the neural correlates that underlie autobiographical, episodic, and semantic memory. Autobiographical memory was defined as the conscious recollection of personally relevant events, episodic memory as the recall of stimuli presented in the laboratory, and semantic memory as the retrieval of factual information and general knowledge about the world. Our objective was to delineate common neural activations, reflecting a functional overlap, *and* unique neural activations, reflecting functional dissociation of these memory processes. We conducted an event-related functional magnetic resonance imaging study in which we utilized the same pictorial stimuli but manipulated retrieval demands to extract autobiographical, episodic, or semantic memories. The results show a functional overlap of the three types of memory retrieval in the inferior frontal gyrus, the middle frontal gyrus, the caudate nucleus, the thalamus, and the lingual gyrus. All memory conditions yielded activation of the left medial-temporal lobe; however, we found a functional dissociation within this region. The anterior and superior areas were active in episodic and semantic retrieval, whereas more posterior and inferior areas were active in autobiographical retrieval. Unique activations for each memory type were also delineated, including medial frontal increases for autobiographical, right middle frontal increases for episodic, and right inferior temporal increases for semantic retrieval. These findings suggest a common neural network underlying all declarative memory retrieval, as well as unique neural contributions reflecting the specific properties of retrieved memories. ■

INTRODUCTION

In recent years, the neural basis of human declarative memory has been the focus of numerous functional neuroimaging studies (for reviews see Gilboa, 2004; Graham, Lee, Brett, & Patterson, 2003; Maguire & Mummery, 1999). These studies have mainly attempted to determine the unique neural underpinnings of the different aspects of declarative memory as they are currently defined. These include *episodic* memory (EM), defined as the conscious recollection of experienced events, usually in the context of stimuli presented in the laboratory, and *semantic* memory (SM), defined as the conscious recollection of factual information and general knowledge about the world (Tulving, 1972). A number of researchers also have explored *autobiographical* memory (AM), which is the conscious reconstruction and recollection of a personally relevant event (Conway & Pleydell-Pearce, 2000).

Conceptually, AM and SM are easily dissociable, with AM being autonoetic, personally relevant, complex, and context-rich. In contrast, SM is generally thought to be free of context and personal relevance. However, such a distinction has proven not to be clear-cut. Most theorists agree that the two types of memory dissociate at some level of neural processing, but a consensus has yet to be reached as to where that would be. One view asserts that hippocampal areas engage AM exclusively (Tulving & Markowitsch, 1998; Vargha-Khadem et al., 1997; Tulving, Hayman, & MacDonald, 1991), whereas another view stresses the interdependence of AM and SM, hence, claiming that the hippocampus is essential for both types of memories (Westmacott & Moscovitch, 2003; Squire & Zola, 1998). Most support for the former argument comes from amnesic patients with hippocampal lesions who show deficits in AM but with their SM spared (Gadian et al., 2000; Hirano & Noguchi, 1998; Vargha-Khadem et al., 1997). On the other hand, there is evidence that hippocampal amnesics exhibit impairments in SM (Manns, Hopkins, & Squire, 2003; Kopelman & Kapur, 2001), suggesting that the hippocampi are critically involved in both types of declarative memory. At a neocortical level, the neural distinction between AM and SM has been fairly well established, with the left inferior prefrontal cortex (PFC) and left posterior temporal areas underlying SM (Graham et al., 2003), and the medial frontal cortex, middle temporal,

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and temporopolar areas subserving AM (Graham et al., 2003; Maguire, Vargha-Khadem, & Mishkin, 2001). Similarly, EM and SM have been differentiated not only in terms of the contents of memory but also in terms of brain activity. Neuroimaging studies show that when the two types of memory are compared with each other, EM activates right prefrontal regions (Duzel, Habib, Guderian, & Heinze, 2004), whereas SM activates left prefrontal areas (Wigs, Weisberg, & Martin, 1999).

In contrast, the distinction between AM and EM is much less clear. For some researchers, AM is conceptualized as synonymous with EM (Nyberg et al., 1996), whereas for others, AM is considered a subsystem of a broader EM system (Piefke, Weiss, Markowitsch, & Fink, 2005; Piefke, Weiss, Zilles, Markowitsch, & Fink, 2003; Tulving & Markowitsch, 1998). Both of these views agree that AM and EM involve conscious recollection of an event and its contextual details. According to such views, as long as the ''what, where, when'' aspects of the retrieved information are present, both AM and EM would involve a similar neural network, thus dissociating very little, if at all, in underlying functional processes. Another perspective, however, draws attention to several characteristics that significantly differentiate AM and EM; specifically, personal relevance, emotional content, and time elapsed between encoding and retrieval (Gilboa, 2004; Wheeler, Stuss, & Tulving, 1997). Proponents of this view argue that material encoded in the laboratory lacks personal significance, is limited in context, and differs in time frame from autobiographical content. Hence, the functional networks underlying AM and EM should dissociate at certain critical brain areas. Recent evidence shows that in the PFC, the two memory functions indeed involve different brain areas, with AM recruiting the ventromedial PFC and EM recruiting the mid-dorsolateral PFC (Gilboa, 2004). Gilboa (2004) has suggested that autobiographical retrieval involves monitoring and verification of internal personal information, mediated by the ventromedial PFC, whereas episodic retrieval entails monitoring of external impersonal information geared toward avoiding mistakes, mediated by the dorsolateral PFC.

As suggested by this brief review, most of the emphasis, to date, has been on exploring the unique aspects of these different types of memory. However, some evidence of functional overlap in general retrieval processes does exist. Common activations have been reported across episodic and working memory tasks (Nyberg et al., 2003; Cabeza, Dolcos, Graham, & Nyberg, 2002; Nyberg, Forkstam, Petersson, Cabeza, & Ingvar, 2002; Braver et al., 2001) and across EM and SM tasks (Rajah & McIntosh, 2005; Nyberg et al., 2002, 2003; Wigs et al., 1999). Neural commonalities among the different types of memory can be interpreted in line with one of the two following views: (1) the view of multiple memory systems (Tulving, 1987), which are believed to be functionally and anatomically independent but *interac-*tive due to shared attentional and/or executive processes mediated by the utilized measures (Nyberg et al., 2002; Cabeza & Nyberg, 2000); or (2) the view of a unitary or common memory network that gives rise to at least some aspects of all memory retrieval (Rajah & McIntosh, 2005; Friston, 2002; McIntosh, 1999; Baddley, 1984). We favor the latter view, which is supported by the following evidence: (1) encoding of to-be-remembered material is almost always contextual (i.e., embedded in already acquired knowledge); only later would some memories become decontextualized (Rajah & McIntosh, 2005; Westmacott & Moscovitch, 2003; Baddley, 1984); (2) autobiographical and episodic retrieval are *not* free of factual, semantic information (Gilboa, 2004); and (3) SM is rarely entirely context-free, but rather may contain some contextual and episodic components, although these may be degraded and lack rich detail (Gilboa, 2004; Westmacott, Black, Freedman, & Moscovitch, 2004; Westmacott & Moscovitch, 2003). We hypothesized that retrieval of the three types of memory likely would involve the recruitment of common neural regions, reflecting an overlap in activation patterns, as well as the recruitment of brain regions unique to each type of declarative memory, reflecting the distinct properties of retrieved information mediated by task-specific functional processes.

The purpose of the present study was to identify those brain areas that are common to AM, EM, and SM, as well as those that are unique to each. We designed our study paradigm so that the visual input (i.e., the retrieval cue) remained the same but the retrieval demand varied across the memory types. Such a paradigm allowed for a direct comparison of the different retrieval types, while holding stimulus presentation constant. In other words, the task was designed to reveal only aspects of memory retrieval, and avoid any confounds introduced by different retrieval cues (e.g., personal photos vs. photos of objects to study AM vs. SM).

We hypothesized that all retrieval types would recruit a common neural network, involving the coactivation of the occipital cortex, thalamus, medial-temporal (hippocampus, in particular), and prefrontal areas. Increased activity in the visual cortex would be expected if visual imagery is involved during retrieval (e.g., Kosslyn et al., 1993), which is likely in both AM and EM, and may occur in SM as well if the retrieval is effortful. We also expected to see thalamic activation for all three types of retrieval as it has been known for some time that thalamic lesions result in deficits in AM and EM (e.g., Kishiyama et al., 2005; Van Der Werf, Jolles, Witter, & Uylings, 2003; Harding, Halliday, Caine, & Kril, 2000). Recently, it has also been found that thalamic lesions lead to problems in semantic retrieval (Miller, Caine, & Watson, 2003). The hippocampus would be involved in AM and EM, as it is thought to be essential in the retrieval of detailed, episodic memories (e.g., Gilboa, Winocur, Grady, Hevenor, & Moscovitch, 2004; Squire & Zola-Morgan,

1991) and memories with a spatio-temporal context (Burgess, Maguire, Spiers, & O'Keefe, 2001). Recent evidence also suggests that the left hippocampus is critical for semantic relational memory (Prince, Daselaar, & Cabeza, 2005). We hypothesized that semantic retrieval is not entirely context-free, but that semantic recollections are interrelated with an existing knowledge base that includes knowledge and memories about the self that can be retrieved along with factual knowledge; hence, semantic recollection should activate the hippocampus. Similarly, retrieval of AM and EM would entail some retrieval of associated semantic knowledge so that the left inferior frontal gyrus (IFG), active for semantic processing (Greenberg et al., 2005; Thompson-Schill, 2003; Wagner, Pare-Blagoev, Clark, & Poldrack, 2001), might be active in all three types of memory retrieval.

In addition to these common regions, we expected to find unique cortical activations for each retrieval type. In particular, we expected to see a dissociation of PFC activity in autobiographical and episodic retrieval, with AM engaging ventromedial frontal areas and EM involving dorsolateral areas of the PFC (Gilboa, 2004). Lastly, we predicted unique temporal activations in semantic retrieval, as some have suggested that semantic representations are stored in specific areas of the posterior temporal cortex (Graham et al., 2003; Chao, Martin, & Haxby, 1999).

METHODS

Participants

Twelve right-handed, healthy young participants (mean age = 26.8 years; range = 21–37 years; 3 men) took part in the study. All participants signed an informed consent that was approved by the ethics boards at Baycrest and Sunnybrook Health Science Centre.

Stimuli

Experimental Stimuli

Fifty color and black-and-white photographs depicting general, everyday events (e.g., driving or camping) as well as one-time but highly publicized occurrences (e.g., the 9/11 attack on the World Trade Center) were used as visual cues for the experimental retrieval conditions. The stimuli were carefully selected to ensure that they would relate to events commonly experienced by the individuals of the selected demographic population, so that most, if not all, stimuli would serve as effective cues for AMs in all participants. Each picture was shown with a one- or two-word descriptive title below it. This was done to direct all participants' attention to the same attribute of the presented stimulus, especially in more complex visual scenes (e.g., a photograph depicting two chairs and a table in a dilapidated environment titled ''Poverty''), thus reducing the variability of the elicited AMs across participants.

Control Stimuli

Five photographs were selected from the set of 50 described above and scrambled using a Matlab script. This ensured that most aspects of the perceptual input remained the same, while rendering the stimulus meaningless.

Procedure

The study consisted of one control and three memory retrieval conditions during functional magnetic resonance imaging (fMRI) scanning. Four 14-min runs of 50 trials each were presented to the participants in a counterbalanced order. Trials were randomized within each run. In each trial, an experimental or control stimulus was shown for 4 sec. Each experimental stimulus was shown three times during the experiment but never in sequence or in the same scanning run. Participants were asked to pay attention to the photograph so that they could successfully answer a subsequently presented question that pertained to the stimulus. After the 4-sec presentation of each picture, a question appeared on the screen with three possible answers. Participants had 10 sec to respond by pressing 1, 2, or 3 on a number pad (see Figure 1 for an example trial). Accuracy of memory retrieval was emphasized over speed, and the participants were instructed *not* to guess. The response period was chosen to provide sufficient time for AM retrieval. According to recent electrophysiological evidence, the range of retrieval times for AM is between 3 and 9 sec, with an average time of 5 sec (Conway, Pleydell-Pearce, Whitecross, & Sharpe, 2003). After the 10-sec response period, there was a 1-sec intertrial interval, followed by the next trial. The three memory conditions were as follows:

1. *Autobiographical condition*, in which the stimulus was followed by a cue designed to elicit a personal memory (e.g., ''Think of the last time you went camping''). Participants were asked to relive the memory as vividly as possible and, subsequently, rate the memory according to its vividness (1 = very vivid, 2 = somewhat vivid, 3 = not vivid at all).

2. *Episodic condition*, in which the stimulus was followed by a question about the photograph itself (e.g., ''In the picture, which you have just seen, what is the color of the tent?''). Participants chose from three answers presented to them (1 or 2 being correct, 3 = I don't know).

3. *Semantic condition*, in which the stimulus was followed by a factual type of question (e.g., ''Are there more than 100 camping grounds in Algonquin Park?''). Responses were made in the same fashion as in the episodic condition.

In the control condition, the presentation of a scrambled photograph was followed by an arbitrary instruction

Figure 1. Example of an experimental trial. Participants viewed a photograph for a duration of 4 sec. After a 1-sec interstimulus interval (a blank screen), a question with three possible answers was displayed for 10 sec. The intertrial interval (a blank screen) was 1 sec. In the above example, the question relates to *semantic* retrieval.
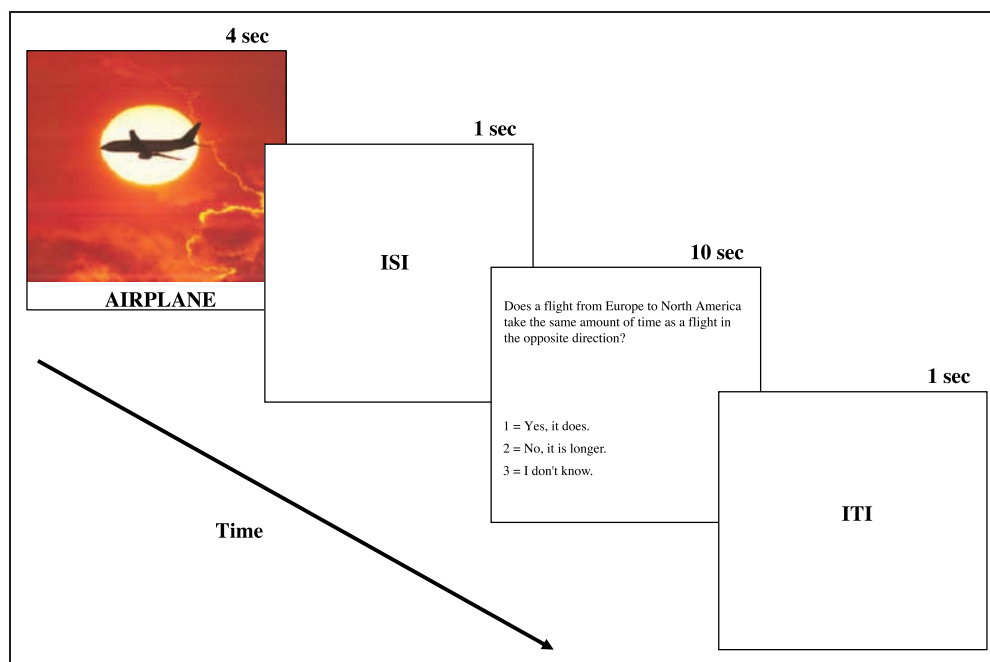
that was *un*related to the stimulus itself (e.g., "Press a key that corresponds to the letter 'C'"). As in the experimental conditions, responses were made by pressing 1, 2, or 3 on a keypad, and the correct key was either 1 or 2.

A postscan interview was administered immediately after the scan session. Participants viewed the 50 photographs again and were asked to describe the AM that had been retrieved during the scan in as much detail as possible. Temporal and spatial information, as well as the content of the event and participant's emotion at the time of its occurrence, were recorded by the experimenter for further analysis.

fMRI Data Acquisition

Anatomical and functional images were collected using a 3-T GE scanner with a standard head coil. For each participant, we acquired a T1-weighted volumetric anatomical MRI (124 axial slices, 1.4 mm thick, FOV = 22 cm). Brain activation was assessed using the blood oxygenation level-dependent effect. For functional imaging, twenty-six 5-mm-thick axial slices were obtained utilizing a T2*-weighted pulse sequence with spiral in–out readout (TR = 2000 msec, TE = 30 msec, FOV = 20, 64 × 64 matrix).

Visual stimuli were presented using fMRI-compatible goggles (Avotec Inc., Stuart, FL) mounted on the head coil. Responses were collected with the Rowland USB Response Box (RURB).

fMRI Data Analysis

Images were reconstructed and preprocessed utilizing the Analysis of Functional Neuroimages (AFNI; Cox,

1996) and Statistical Parametric Mapping (SPM99) software. The images were coregistered to account for head motion of the participants (head motion did not exceed 1.2 mm). Furthermore, the images were normalized to a standard space using a linear transformation with sinc interpolation. Lastly, the data were smoothed with a 6-mm Gaussian filter.

Image data were analyzed with partial least squares (PLS; McIntosh, Chau, & Protzner, 2004; McIntosh, Bookstein, Haxby, & Grady, 1996) to identify regional activity change as a function of task (i.e., type of memory retrieval) demands. PLS identifies those voxels whose signal change covaries with the experimental conditions in the same way; that is, those regions which covary *together* across the conditions. This multivariate approach is similar to a principal component analysis (e.g., Friston, Frith, & Frackowiak, 1993) and assumes that brain function reflects the coordinated activity of groups of brain regions rather than the independent activity of any single brain region. An additional advantage of this technique is that all task conditions can be entered simultaneously into the analysis, thus facilitating the identification of common patterns of brain activity across conditions, as well as patterns unique to specific retrieval conditions. The output of PLS analysis is a set of latent variables (LVs), components reflecting cohesive patterns of brain activity related to the experimental design.

In the PLS analysis, we included those trials for semantic, episodic, and control conditions for which participants made a correct response and all "very vivid" and "somewhat vivid" trials for autobiographical condition. The average number of correct experimental trials was 27 for the semantic condition, 31 for the episodic

condition, and 42 for the autobiographical condition per participant. (Note that the number of autobiographical trials is larger, as both "very vivid" and "somewhat vivid" trials were considered successful memories.) Because our chief interest was in brain activity during memory *retrieval*, not in how activity was modulated by the cue, we isolated activity during retrieval by conducting the analysis on the 16-sec period, starting at the onset of the question following each picture presentation (i.e., 8 TRs). In addition, activity at each time point in the analysis was normalized to activity in the first TR of the question period (labeled TR0 in the figures), and thus, our measure of retrieval-related activity was relatively uninfluenced by cue activity. PLS as applied to event-related data results in a set of brain regions related to the task contrasts for each TR on each LV (McIntosh et al., 2004). For each TR, a "brain score" is calculated for each participant that is an index of how strongly that participant shows the particular pattern of brain activity identified for that TR. To determine contrasts across conditions, mean brain scores were plotted across the 8 TRs used in the analysis (Figure 2). These plots show how the pattern of activity across the brain is

expressed over the 16-sec retrieval period, and are analogous to hemodynamic response functions that are typically plotted for individual brain regions. The significance for each LV as a whole was determined by using a permutation test (McIntosh et al., 1996). As 500 permutations were used, the smallest p value obtainable for each LV was $p < .002$. In addition to the permutation test, a second and independent step was to determine the reliability of the saliences (or weights) for the brain voxels characterizing each pattern identified by the LVs. To do this, all saliences for each TR were submitted to a bootstrap estimation of the standard errors (Efron & Tibshirani, 1985). Peak voxels with a salience/SE ratio >3.0 were considered to be reliable, as this approximates $p < .005$ (Sampson, Streissguth, Barr, & Bookstein, 1989). Local maxima for the brain areas with reliable saliences on each LV were defined as the voxel with a salience/SE ratio higher than any other voxel in a 2-cm cube centered on that voxel. Because PLS uses images in the format developed by the Montreal Neurological Institute (MNI), all coordinates resulting from the PLS analyses were converted from MNI space to Talairach coordinates using the algorithm developed by
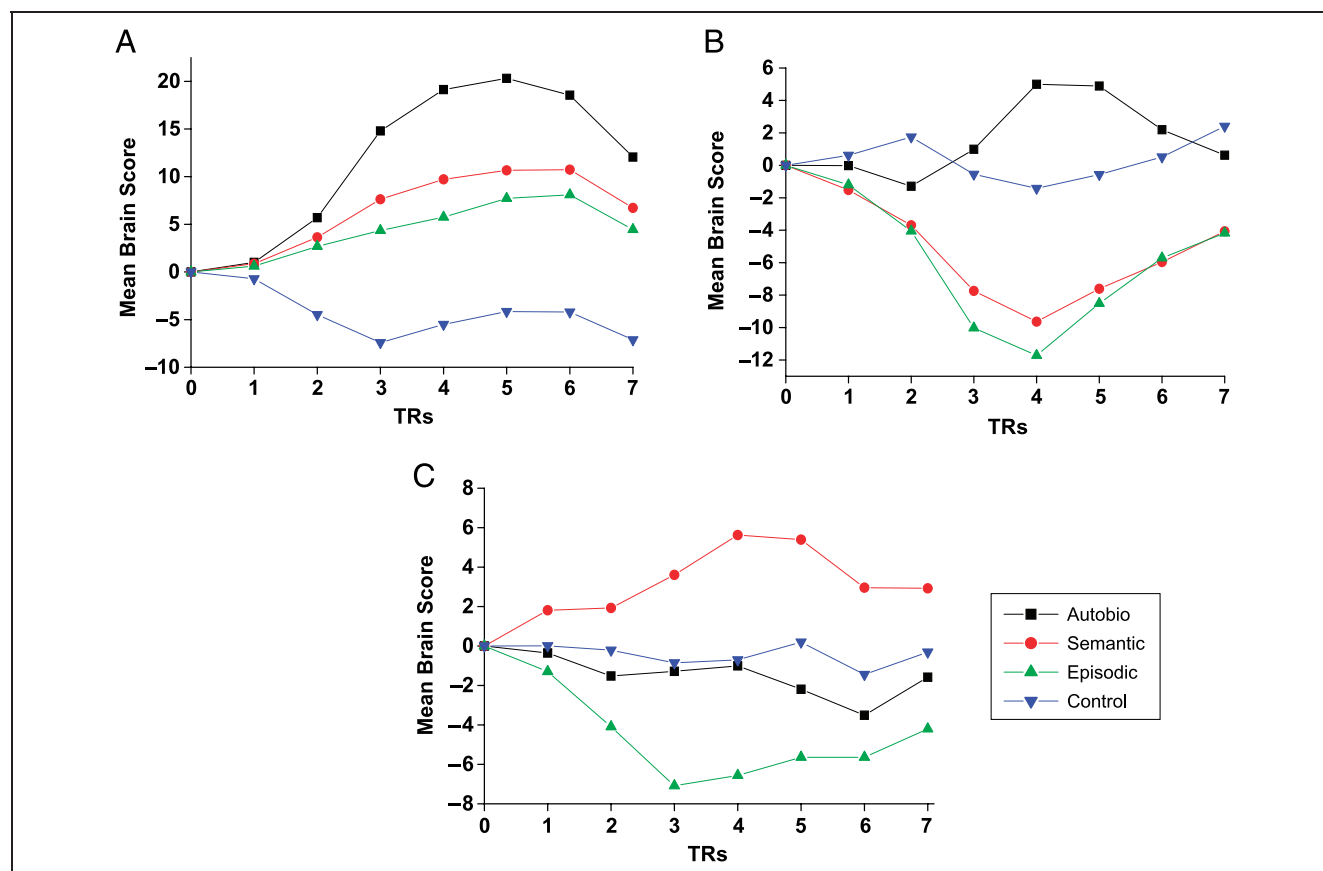
Figure 2. Changes in brain activity related to task over time. For each latent variable (LV), mean brain scores (summed scores of activity across the entire brain of each participants and averaged across participants) were plotted for each condition (AM = black; SM = red; EM = green; control = blue) over 7 time points (TRs; each TR equals 2 sec). (A) LV1 ($p < .01$) shows a functional differentiation between all the retrieval tasks and control (with AM showing the greatest difference from control); (B) LV2 ($p < .01$) differentiates AM from both SM and EM; (C) LV3 ($p < .10$) shows EM differing from SM, whereas both AM and control are roughly at zero.

Brett and colleagues (www.mrc-cbu.cam.ac.uk/Imaging/Common/mnispace.shtml). The clusters reported here contained at least 5 voxels (i.e., 400 μl), and most were taken from the bootstrap results for the fifth or sixth TR (i.e., at 8–12 sec after stimulus onset). A single TR was selected as a representative index of brain activity in time, although most regions reported in this article showed reliable activations across multiple time points.

RESULTS

Behavioral Performance

Behavioral performance was assessed by comparing the means of the response times across the four conditions (correct trials only), using a repeated-measures ANOVA. The effect of condition was highly significant, $F(3,33) = 73.1$, $p < .001$. Pairwise t tests with Bonferroni corrections for multiple comparisons showed that the response times for autobiographical retrieval ($M = 6989$ msec, $SD = 1478$) differed significantly from that for the control task ($M = 1925$ msec, $SD = 728$) and episodic retrieval ($M = 4640$ msec, $SD = 1150$, both at $p < .01$). The difference in reaction time (RT) for autobiographical retrieval and semantic retrieval ($M = 5858$ msec, $SD = 1366$) approached significance ($p = .06$).

fMRI Results

The first two LVs from the task PLS analysis were significant at $p < .01$, and the third LV showed a trend at $p < .10$. LV1, which accounted for 65% of the variance in the data, identified brain regions differentiating all of the memory conditions from control, with the largest difference between the autobiographical and control conditions (Figure 2A). The second LV accounted for 21% of variance in the data and showed differentiation of the autobiographical condition from both semantic and episodic retrieval conditions (Figure 2B). Lastly, LV3 (Figure 2C) accounted for 14% of the variance and yielded an activation pattern mainly differentiating semantic and episodic retrieval, although autobiographical retrieval shared some common activity with EM on this LV. For clarity, the brain regions identified by the LVs are discussed in terms of common and unique activations for the three memory conditions.

Activations Common across the Three Memory Conditions

The significant activations that differentiated all three types of retrieval from the control condition are shown in Table 1. These included the IFG and the thalamus, bilaterally. Increased activity across all memory trials also was seen in the right caudate nucleus, and the lingual and middle frontal gyri in the left hemisphere (Figure 3).

Table 1. Activations in All Retrieval Conditions versus Control Condition

| Region | Hem | BA | Talairach Coordinates | | | Ratio |
			x	y	z	
Inferior FG	L	47	−44	27	−8	8.9
	R	47	48	19	−8	5.4
Middle FG	L	8	−40	10	47	9.2
Caudate nucleus	R		12	15	−4	6.2
Thalamus	L		−8	−15	8	9.5
	R		12	−4	8	6.1
Lingual gyrus	L	18	−4	−70	3	4.9

Hem = hemisphere; R = right; L = left; BA = Brodmann's area; Ratio = salience/SE ratio from the bootstrap analysis; FG = frontal gyrus; x coordinate = right/left; y coordinate = anterior/posterior; z coordinate = superior/inferior.

All reported activations in this table are from LV1.

Decreased activity in the memory retrieval conditions, compared to control, was seen in lateral regions of the posterior cortex, including areas of the extrastriate cortex. These decreases in visual regions were due to more activity for the photographs compared to the control stimuli during the preceding cue period. As all activity was normalized to the first time point in the retrieval period, the declining extrastriate activity in the memory conditions was greater than that seen during the control condition, resulting in more apparent activity during the control condition.

Other Areas of Overlap

The second LV identified multiple regions of the left medial-temporal lobe (MTL) with contributions to memory retrieval (Figure 4). There was a region of the left hippocampus that showed increased activity for both EM and SM (Figure 4A) and a decrease in activity during AM. A more ventral region of the left parahippocampal gyrus showed increased activity only for AM (Figure 4C). An intermediate region between these two maxima showed an increase in activity for all three memory conditions compared to control (Figure 4B). Thus, the left medial-temporal region showed both common and unique contributions to memory retrieval.

LV2 also identified areas that showed a clear functional differentiation of SM and EM from AM. These areas of overlap between semantic and episodic retrieval included two regions in the right frontal lobe, one in the dorsomedial PFC and the other in the ventrolateral PFC (BA 8 and BA 11, respectively; see Table 2 and Figure 5A). A third region with increased activity only in SM and EM was seen in the left fusiform gyrus (Table 2). Areas of common activation in autobiographical and episodic
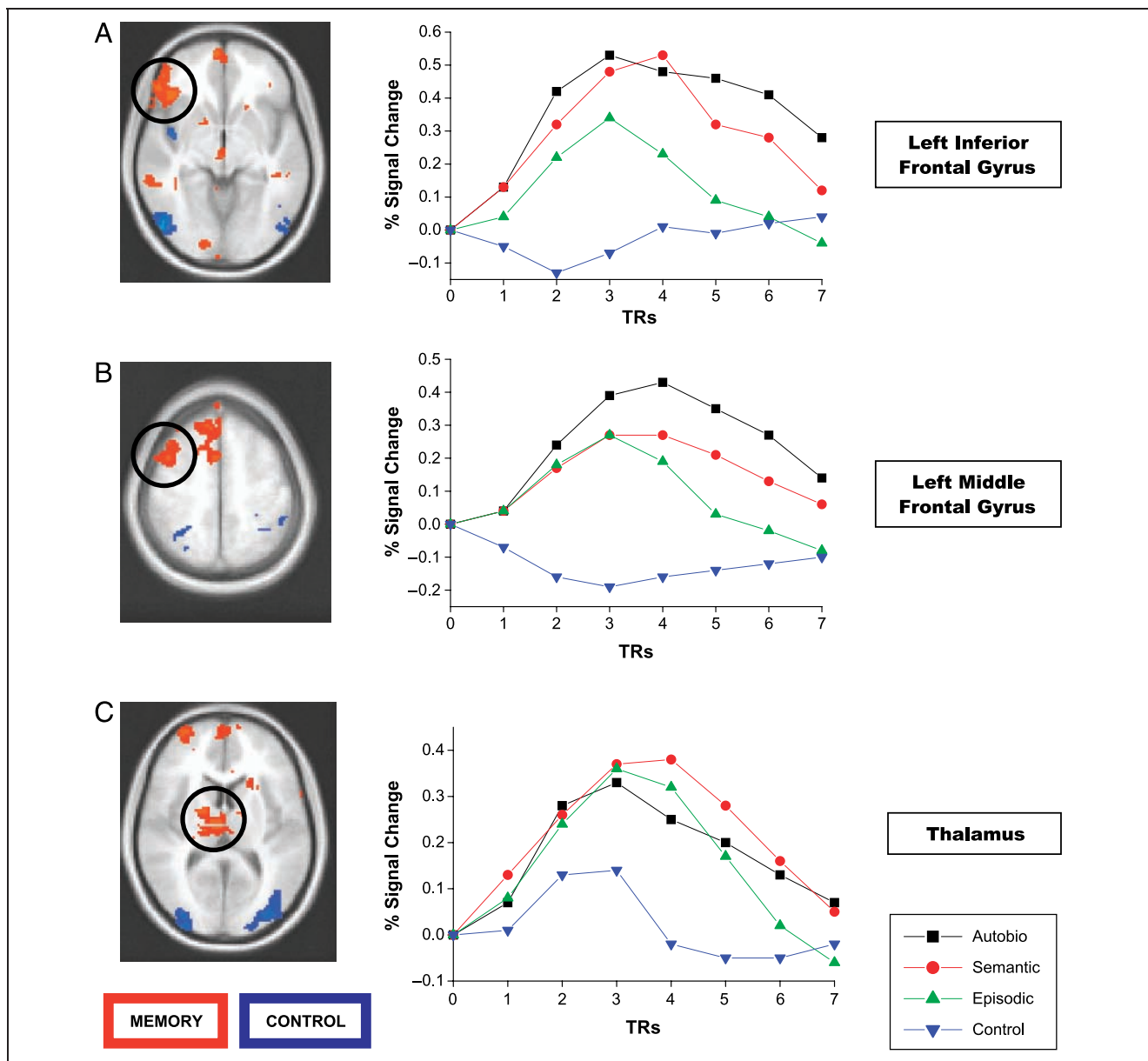
Figure 3. Activations common across all memory conditions. Areas in which activity was increased during all types of memory retrieval are shown on the MNI average brain (the right hemisphere is on the right side of the images; see also Table 1). Red areas represent those with increased activity during memory tasks relative to control, whereas blue areas represent those with decreased activity during memory retrieval relative to control. Time courses of activity, expressed as the percentage of signal change relative to the first TR, were plotted over the 7 TRs after the onset of the question stimulus for the left inferior frontal gyrus (A), left middle frontal gyrus (B), and thalamus (C). These regions are indicated by black circles. Note: in this and all following figures, circled areas of interest are shown in red for better visualization, despite some having a negative salience on a given LV.

retrieval were found bilaterally (in LV3) in the inferior parietal cortices (Figure 5B).

Activations Unique to Each Memory Condition

Table 3 shows activations unique to each memory condition. As noted above, LV1 indicated that the AM condition showed the largest difference from control. Inspection of the time courses from the areas identified by this LV revealed that some regions appeared to have

increased activity only for the AM condition. In particular, autobiographical retrieval appeared to uniquely activate two regions in the anterior (Figure 6A) cingulate gyrus, the posterior cingulate gyrus, and the left middle frontal gyrus. To determine whether activity was unique to AM, we carried out a series of *t* tests contrasting the memory conditions to control and then contrasting AM to both EM and SM for each of these regions. For all of the four regions, activity in the AM condition was significantly higher than activity in the EM, SM, and control
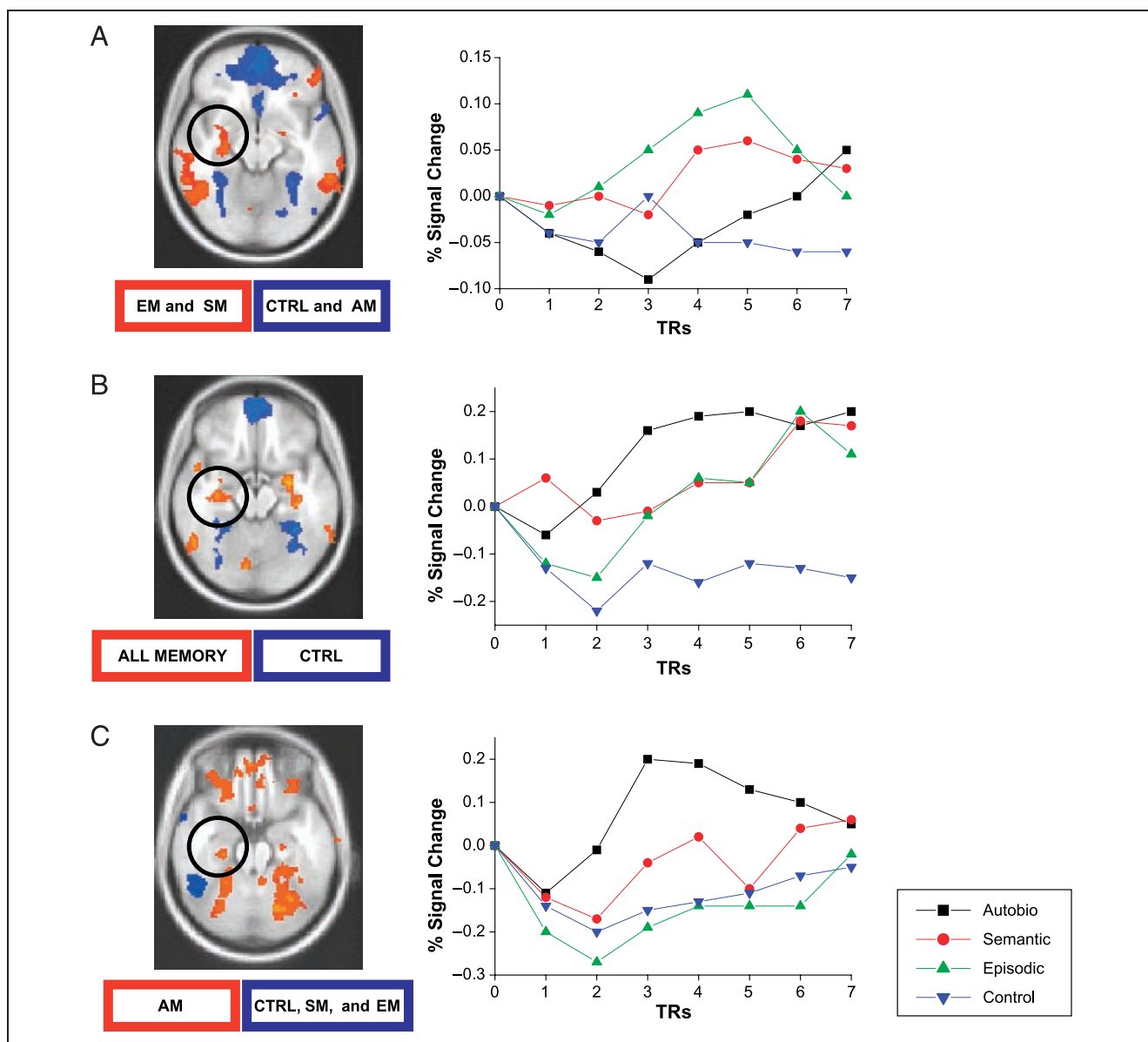
Figure 4. Activations in the left MTL. Medial temporal areas where activity was increased during memory retrieval (indicated by black circles) are shown on the MNI average brain. All three MTL areas are from LV2. Time courses of activity were plotted as in Figure 3. (A) A superior MTL area, with coordinates at $x = -28$, $y = -12$, $z = -13$ was active in SM and EM relative to control and AM; (B) A more posterior and inferior MTL area, with coordinates at $x = -28$, $y = -20$, $z = -16$ was active in all memory conditions relative to control, with AM showing a more rapid increase in activation, and EM and SM showing more gradual increases in activity; (C) A ventral MTL area, with coordinates at $x = -24$, $y = -24$, $z = -19$ was active only during AM relative to the rest of the conditions.

conditions ($p < .05$, corrected for multiple comparisons), and activity during EM or SM was *not* significantly increased above the control condition for any region. Additional regions unique to AM were identified by LV2, including the right ventromedial frontal cortex and the middle frontal gyrus, as well as the bilateral insula (Table 3).

Finally, LV3 identified some areas that were unique to either EM or SM (see Table 3). Episodic retrieval engaged the left superior parietal lobule (Figure 6B), the right middle frontal gyrus, the dorsomedial PFC, and the left precuneus. Semantic retrieval engaged two regions

in the right middle frontal gyrus and an area of the right inferior temporal gyrus (Figure 6C) exclusively.

DISCUSSION

In the present study, we contrasted brain activations that underlie three different types of declarative retrieval, namely, autobiographical, episodic, and semantic. As predicted, we found a common pattern of brain activity underlying all the retrieval conditions, as well as activations common to two types of retrieval or unique to only one memory type. These results provide evidence that at

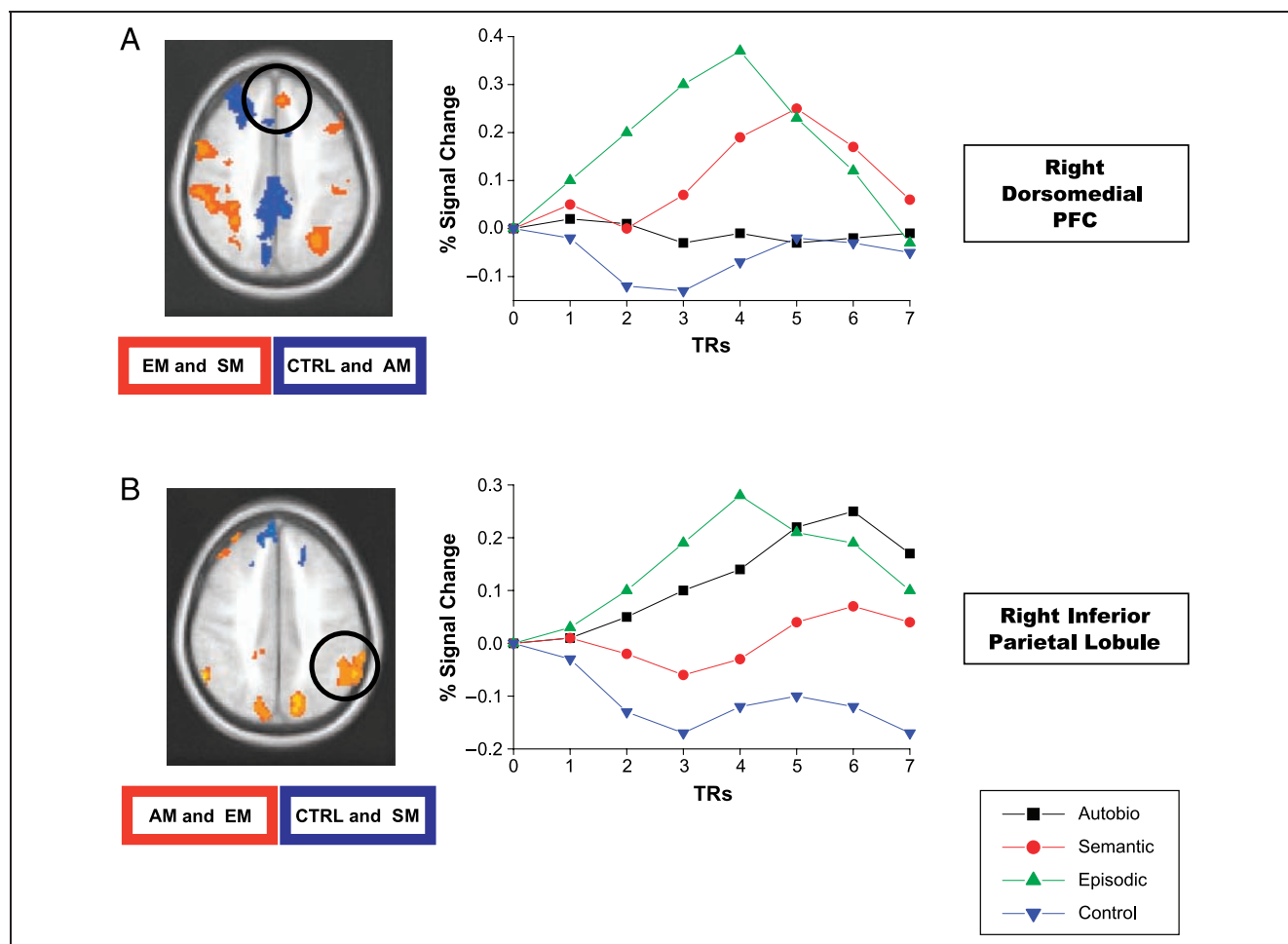**Table 2.** Areas with Increased Activity in Two of the Three Memory Conditions

Region	Hem	BA	x	y	z	Ratio	LV
Semantic and episodic							
Dorsomedial PFC	R	8	4	41	35	−8.4	2
Ventrolateral PFC	R	11	52	46	−16	−6.1	2
Fusiform gyrus	L	37	−52	−55	−14	−7.5	2
Autobiographical and episodic							
Inferior parietal lobule	R	40	59	−49	36	−6.5	3
	L	40	−55	−53	36	−6.2	3

Hem = hemisphere; R = right; L = left; BA = Brodmann's area; Ratio = salience/SE ratio from the bootstrap analysis; PFC = prefrontal cortex; LV = latent variable; *x* coordinate = right/left; *y* coordinate = anterior/posterior; *z* coordinate = superior/inferior.

least some aspects of AM, EM, and SM are carried out by the same brain regions, despite the common conception of these types of memory as distinct from one another.

Common Memory System

Regions active across all memory trials included the left lingual gyrus, the thalamus, the caudate nucleus, the left middle frontal gyrus, the IFG, and the left hippocampus. Activations in the lingual gyrus may underlie the maintenance in working memory of visual information relevant to the memory retrieval (e.g., Ragland et al., 2002) or visual imagery recruited to assist in retrieval of memory details (Mazard, Laou, Joliot, & Mellet, 2005; Kosslyn et al., 1993). The thalamus and the caudate nucleus are two of the main nodes in the thalamo-striatal-cortical pathway, which is thought to also underlie working memory maintenance (Ashby, Ell, Valentin, & Casale, 2005; Gazzaley, Rissman, & D'Esposito, 2004), as well as other aspects of memory retrieval (e.g.,

Figure 5. Activations common to two memory conditions. Areas with increased activity common to two memory retrieval conditions (indicated by black circles) are shown on the MNI average brain (see also Table 2). Time courses of activity were plotted as in Figure 3. (A) Increased activity in the right dorsomedial PFC was found in both SM and EM relative to control (from LV2); (B) Increased activity in the inferior parietal lobule, bilaterally, was found in both AM and EM relative to control (from LV3). The time course plots the hemodynamic response from the right hemisphere.

Table 3. Activations Unique to Each Memory Condition

Region	Hem	BA	Talairach Coordinates			Ratio	LV
			x	*y*	*z*		
Autobiographical							
Anterior CG	L	32	−4	21	28	9.0	1
	R	24	4	36	17	4.7	1
Posterior CG	L	31	0	−58	14	8.1	1
Insula	L	13	−40	11	−4	7.8	2
	R	13	44	11	−4	6.9	2
Middle FG	L	10	−32	58	4	6.1	1
	R	10	32	51	20	9.5	2
Ventromedial FG	R	10	4	63	8	9.3	2
		11	8	60	−12	13.7	2
Episodic							
Middle FG	R	10	36	54	−3	−5.1	3
Medial FG	R	8	4	41	38	−8.1	3
Superior PL	L	7	−44	−56	54	−5.7	3
Precuneus	L	7	−8	−71	48	−7.5	3
Semantic							
Middle FG	R	9	20	41	35	6.1	3
	R	8	40	18	43	5.2	3
Inferior TG	R	20/21	67	−13	−23	5.7	3

Hem = hemisphere; R = right; L = left; BA = Brodmann's area; Ratio = salience/SE ratio from the bootstrap analysis; CG = cingulate gyrus; FG = frontal gyrus; PL = parietal lobule; TG = temporal gyrus; LV = latent variable; *x* coordinate = right/left; *y* coordinate = anterior/posterior; *z* coordinate = superior/inferior.

Kishiyama et al., 2005). In addition, recent evidence suggests the involvement of both the thalamus and caudate nucleus in the activation of internal object representations (Kraut et al., 2002). Thus, it is reasonable that these areas would be involved in all three experimental conditions, as all would involve working memory maintenance and retrieval of object representations to some extent.

Interestingly, we found left hippocampal activation across *all* declarative retrieval conditions, although functional dissociations *within* the MTL, with anterior/superior parts subserving EM and SM and posterior/inferior parts subserving AM retrieval, indicate some regional specialization on the basis of the specific type of information that is retrieved. Nevertheless, our data suggest that some part of the left MTL is involved in declarative retrieval, regardless of the specific information retrieved. This would be expected for EM and AM, based on ear-

lier findings, but less expected for SM, according to some current theories of MTL function (e.g., Tulving & Markowitsch, 1998; Vargha-Khadem et al., 1997). On the other hand, the finding of the left MTL activation for SM is consistent with other theories that emphasize the role of this area in both EM and SM (e.g., Prince et al., 2005). It may be possible to reconcile these two views, and explain our results, if one considers that MTL activation in any memory retrieval task would depend both on the task demands specified by the experimenter and the additional processes that an individual participant would bring to bear, even if not asked to do so. That is, our task was similar to a ''real-world'' retrieval event and may have encouraged retrieval of episodic and/or autobiographical details along with the semantic information requested, accounting for MTL activation during the SM trials. Further support for this idea comes from the involvement of the hippocampus in recollective processes (Cabeza et al., 2004; Eldridge, Knowlton, Furmanski, Bookheimer, & Engle, 2000). Activation of the left MTL across all memory types here is consistent with the idea that some recollection occurred regardless of the actual type of information requested on any given trial. Thus, our results would suggest that contextual information is frequently retrieved along with semantic information in real-world situations, and perhaps under other experimental conditions as well, leading to somewhat variable involvement of MTL structures in memory experiments.

As to the PFC, the IFG have been implicated in response inhibition and selection control (e.g., Brass, Derrfuss, Forstmann, & von Cramon, 2005; Aron, Robbins, & Poldrack, 2004; Liddle, Kiehl, & Smith, 2001), as well as in top-down attentional control (Banich et al., 2000). Some evidence supports hemispheric differentiation in that the left IFG was found to process semantic information exclusively (Moss et al., 2005), whereas the right IFG was linked to autobiographical retrieval only (Greenberg et al., 2005). Nyberg et al. (2002) found increased activity in the right inferior cortex associated with episodic retrieval, whereas increased activity in the left inferior cortex was linked to a functional overlap of autobiographical, episodic, and working memory retrieval. Similarly, we found increased activity in both the left and right IFG during all three retrieval conditions, suggesting engagement of these areas for declarative memory in general, with no hemispheric asymmetry. This result supports our argument that AM, EM, and SM overlap to a large degree due to *some* properties of the retrieved content (e.g., AM and EM include some semantic information and SM is rarely void of contextual information), hence, would engage similar inhibitory and/or response selection processes.

Activations Shared across Two Memory Conditions

Both semantic and episodic retrieval were differentiated from autobiographical retrieval in the right dorsomedial
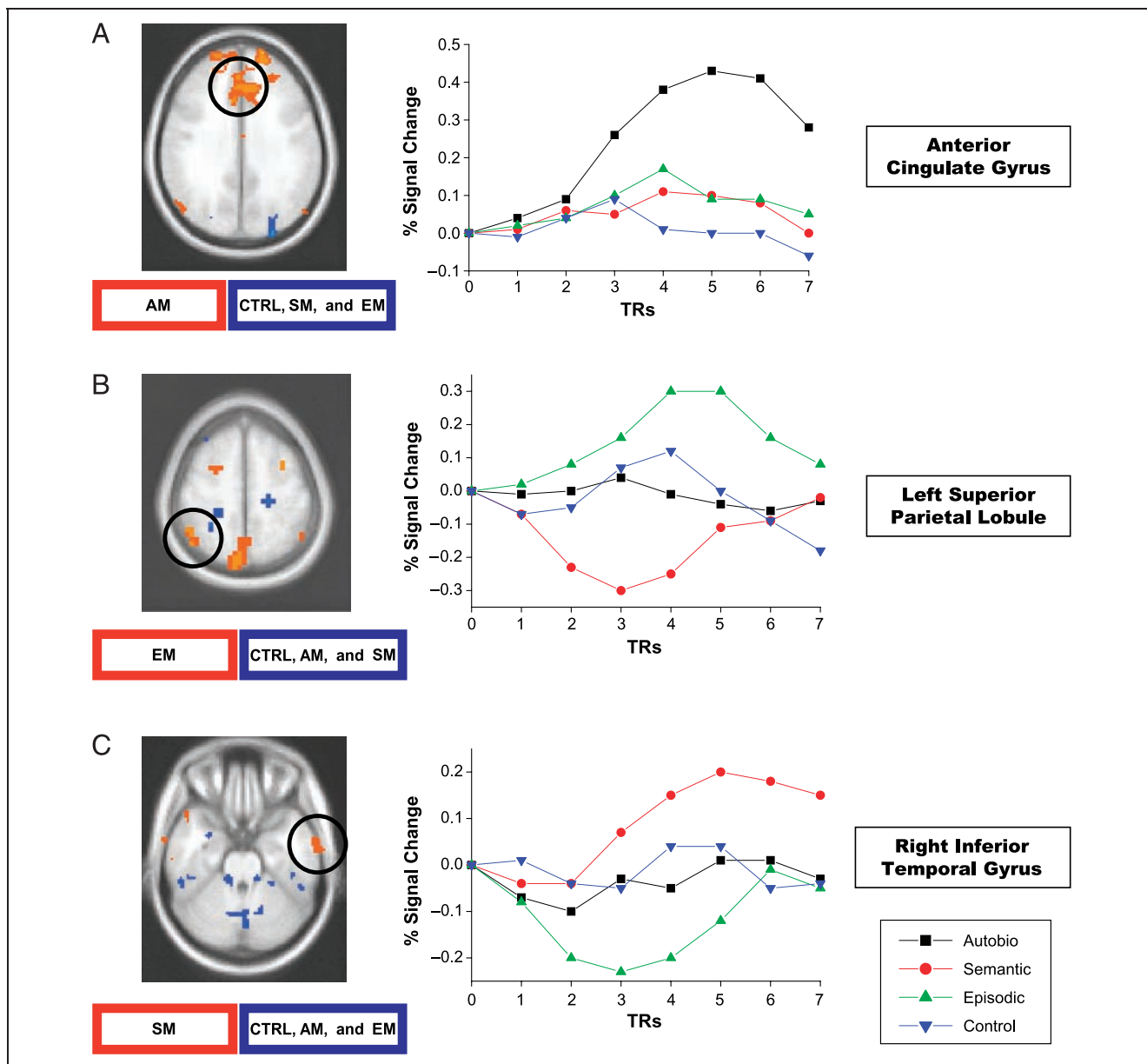
Figure 6. Activations unique to each memory retrieval type. Areas with increased activity in only one memory retrieval condition (indicated by black circles) are shown on the MNI average brain (see also Table 3). Time courses of activity were plotted as in Figure 3. (A) Increased activity in the anterior cingulate gyrus was found only in autobiographical retrieval (from LV1); (B) Increased activity in the left superior parietal lobule was shown only in episodic retrieval (from LV3); (C) Increased activity in the right inferior temporal gyrus was unique to semantic retrieval (from LV3).

and ventrolateral areas of the PFC, both of which have been linked to working memory processes (e.g., Mottaghy, Gangitano, Sparing, Krause, & Pascual-Leone, 2002). This suggests that some aspects of working memory maintenance are more functionally robust in EM and SM, compared to AM. In addition, we found a differentiation of SM and EM from AM in the left fusiform gyrus, which has been linked to object recognition (Garoff, Slotnick, & Schacter, 2005), as well as visual imagery of concrete objects (Hua, Lui, Yang, & Lei, 2005), suggesting that maintenance of the cue stimulus during the retrieval period occurred more frequently for

SM and EM than for AM. Episodic and autobiographical retrieval shared common activation in the lateral areas of the inferior parietal lobule, bilaterally. Recent evidence shows that activity in the parietal regions is an index of memory retrieval, particularly in recognition studies where it is more active when judging stimuli to be "old" rather than "new" (Henson, Hornberger, & Rugg, 2005; Wagner, Shannon, Kahn, & Buckner, 2005). In addition, activity in the left lateral parietal cortex is modulated by the subjective experience of episodic recollection. Specifically, activity increases have been found for items accompanied by detailed recollection

compared to items accompanied only by a feeling of familiarity (Wheeler & Buckner, 2004). Our finding of activity in this area in both AM and EM is consistent with these earlier findings, given that recollective experiences are likely to occur in both conditions. In addition, our result suggests that activity in this area is not modulated by the age of the retrieved memory, whether newly acquired in the laboratory or laid down months or years earlier, consistent with Wheeler and Buckner's (2004) findings.

Unique Activations

Finally, we found activations unique to each memory type, in line with the idea that there are specific properties that distinguish memory retrieval events. Autobiographical retrieval, which differs from EM and SM in that it involves re-experiencing of personally relevant events and likely involves retrieval of more contextual details, was accompanied by increased activity in the anterior and posterior cingulate gyri, insula, bilateral middle frontal gyri, and ventromedial PFC. The differences that we found in PFC activity between AM and EM were consistent with the idea that different PFC regions mediate qualitatively different monitoring strategies during memory retrieval (for a review, see Gilboa, 2004). Autobiographical retrieval involved the ventromedial PFC (BA 10/11), which is believed to be related to self-reference (Fossati et al., 2003) and monitoring of the authenticity of self-relevant recollections (Gilboa, 2004). Episodic retrieval, on the other hand, engaged the anterior portion of the middle frontal gyrus (BA 10), which is thought to mediate monitoring of retrieval responses related to external in-laboratory encoded stimuli and retrieval mode (Rugg, Henson, & Robb, 2003; Lepage, Habib, Cormier, Houle, & McIntosh, 2000). Our results are thus consistent with the idea of differential monitoring processes carried out by these two PFC regions.

Increased activity in the anterior cingulate cortex (ACC) and insula, bilaterally, also were found in autobiographical retrieval. The ACC has been implicated in a variety of cognitive and emotional processes (e.g., Critchley et al., 2003; Bush et al., 1998), particularly due to its anatomical and functional connections with both the limbic and prefrontal cortices. AM activated the ventral and rostral areas of the ACC, which are anatomically interconnected with the limbic regions, suggesting their involvement in emotional components of autobiographical recollection. Similarly, the insula has been implicated in memory retrieval of emotional information, as reflected in retrieval of traumatic flashbacks in patients with posttraumatic stress disorder (Osuch et al., 2001), as well as in retrieval of emotionally relevant context in healthy individuals (Smith, Henson, Rugg, & Dolan, 2005). Thus, activations in both the insula and rostral ACC during autobiographical retrieval likely underlie those personally relevant memories that are modulated by emotion.

In addition to the activation of the lateral inferior parietal lobules in both AM and EM, we also found a difference between the two memory types in other parts of the parietal lobe. Increased activity in the posterior cingulate gyrus (BA 31) was found to underlie autobiographical retrieval, whereas increased activity in the left precuneus and superior parietal lobule (BA 7) was evident in episodic retrieval. The role of the posterior parietal cortices in declarative memory is poorly understood but our finding of posterior cingulate activity during AM is consistent with a number of AM studies in recent years (Gilboa et al., 2004) and supports recent evidence that the posterior cingulate is involved in the recollection of personally familiar places and objects (e.g., Sugiura, Shah, Zilles, & Fink, 2005) due to its involvement in retrieval of spatial context (e.g., Burgess et al., 2001). In contrast, the superior parietal lobule aids object maintenance and manipulation of recently encoded stimuli, regardless of personal relevance (Postle, Awh, Jonides, Smith, & D'Esposito, 2004). Also, the precuneus is frequently active during laboratory EM tasks (e.g., Wagner et al., 2005; Cabeza & Nyberg, 2000) and is thought to mediate spatial working memory and imagery (Knauff, Mulack, Kassubek, Salih, & Greenlee, 2002).

Lastly, semantic retrieval showed distinct activations in the right inferior temporal and middle frontal gyri. The right inferior temporal gyrus has been implicated in accessing word meaning (e.g., Sharp, Scott, & Wise, 2004) and underlying the neural representation of conceptual knowledge (Postler et al., 2003; Devlin et al., 2002). Together with the right superior PFC, the right temporal gyrus has been implicated in processing of unique and creative semantic relations (Seger, Desmond, Glover, & Gabrieli, 2000). Considering the design of our study, encouraging an active search for the factual information, we suggest that the participants utilized associative semantic strategies subserved by this right hemispheric network.

Finally, although differences in RT also were noted across retrieval trials, it is unlikely that differences in "time on task" reflected by these RTs accounted for the patterns of brain activity that were observed. We found activity common to all retrieval conditions despite differences in RT across these conditions, and the peak of activity as well as the magnitude of activity in these regions was similar (see Figure 3). Thus, although the amount of time taken to respond differed across the memory conditions, these RT differences did not appear to have any systematic influence on the patterns of brain activity that we observed. This is not to say that RT has no influence at all on brain activity, as some of the regions found here do seem to show differences in how rapidly the hemodynamic response peaks after question onset that might be related to RT differences (for example, see Figure 5). However, it is more likely that the overall patterns of activity seen here are due to commonalities and differences in task demands and the types of information inherent to each memory condition.

In conclusion, we found, as expected, that a number of neural areas are involved in declarative retrieval in general, regardless of the specificity of the recalled information. Our data show strong evidence for a common retrieval network, involving temporo-frontal and thalamo-striatal-cortical circuits that subserve all memory retrieval, and highlight the importance of exploring commonalities among memory types, as well as differences. The differences noted among the memory retrieval conditions indicate that despite the shared functional circuitry, in line with the literature on distinct memory systems, each type of declarative retrieval entails processes that are unique to the nature of the retrieved memory. We conclude that theories of declarative memory will need to be expanded to consider both the general processes involved in the retrieval of any stored information as well as those specific to the particular characteristics of that information.

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