Brain Activity during Episodic Retrieval of Autobiographical and Laboratory Events: An fMRI Study using a Novel Photo Paradigm

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Abstract

■ Functional neuroimaging studies of episodic memory retrieval generally measure brain activity while participants remember items encountered in the laboratory (''controlled laboratory condition'') or events from their own life (''open autobiographical condition''). Differences in activation between these conditions may reflect differences in retrieval processes, memory remoteness, emotional content, retrieval success, self-referential processing, visual/spatial memory, and recollection. To clarify the nature of these differences, a functional MRI study was conducted using a novel ''photo paradigm,'' which allows greater control over the autobiographical condition, including a measure of retrieval accuracy. Undergraduate students took photos in specified campus locations (''controlled autobiographical condition''), viewed in the laboratory similar photos taken by other participants (controlled laboratory condition), and were then scanned while recognizing the two kinds of photos. Both conditions activated a common episodic memory network that included medial temporal and prefrontal regions. Compared with the controlled laboratory condition, the controlled autobiographical condition elicited greater activity in regions associated with self-referential processing (medial prefrontal cortex), visual/spatial memory (visual and parahippocampal regions), and recollection (hippocampus). The photo paradigm provides a way of investigating the functional neuroanatomy of real-life episodic memory under rigorous experimental control. ■

INTRODUCTION

Episodic memory retrieval refers to remembering personally experienced past events (Tulving, 1983). The cognitive and neural mechanisms of episodic memory retrieval have been usually investigated in two different kinds of conditions: participants are asked to remember ''micro-events'' encountered in the laboratory, such as pictures they saw on a computer screen, or they are asked to remember events from their own lives, such as places they visited during summer holidays. Encoding circumstances are typically controlled in the former case but open in the latter, and thus, we call these two conditions ''Controlled Laboratory'' (CL) and ''Open Autobiographical'' (OA). Although most functional neuroimaging studies of episodic retrieval have investigated CL conditions (for reviews, see Rugg & Henson, 2002; Cabeza & Nyberg, 2000), a small group of recent studies have examined OA conditions (for a review, see Maguire, 2001). The results of these two groups of studies produce generally similar results, but differences in the frequency of certain activations across studies have been noted (e.g., Maguire, 2001). For example, prefrontal cortex (PFC) activations tend to be right lateralized or bilateral in CL studies but they are often left lateralized in OA studies. Also, left hippocampal, medial PFC, and amygdalar activations seem to be more frequent in OA than in CL studies. These activation differences are likely due to factors that differ between OA and CL conditions.

Table 1 lists seven factors distinguishing ''typical'' OA and CL conditions, as well as brain regions that have been associated with these factors. They differ both in amount and the degree to which these factors vary, variation that can lead to distinctiveness among the items to be retrieved. (1) Regarding the ''proportion of retrieval processes,'' whereas information production processes tend to be more demanding in OA conditions (particularly when Crovitz's cue–word technique is employed), monitoring/verification processes tend to be more demanding in CL conditions (because they typically assess retrieval accuracy). Given that production processes have been associated with left PFC activity, and monitoring processes with right PFC activity (Cabeza, Locantore, & Anderson, 2003; Allan, Dolan, Fletcher, & Rugg, 2000; Henson, Shallice, & Dolan, 1999; Rugg,

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Table 1. Factors Showing Differences between Typical Autobiographical and Laboratory Episodic Retrieval Conditions

Factors	*Typical OA Condition*	*Typical CL Condition*	*CA Condition in This Study*	*Hypothetical Regions Involved*
1. Proportion of retrieval processes	Production: Higher; Monitoring: Lower	Production: Medium; Monitoring: Medium	Production: Medium; Monitoring: Medium	Production: Left PFC; Monitoring: Right PFC
2. Age of memories	Recent to remote	Recent	Recent	Hippocampus
3. Emotional content	Higher	Low	Low	Amygdala, orbito-frontal cortex
4. Retrieval success	Unknown	Accuracy measured	Accuracy measured	PFC, MTL, parietal cortex, precuneus
5. Self-referential processing	Higher	Medium	Higher	Medial PFC
6. Visual/spatial memory	Higher	Medium	Higher	Visual and parahippocampal cortex
7. Recollection	Higher	Medium	Higher	Hippocampus

Fletcher, Allan, et al., 1998), this factor could account for differences in the lateralization of PFC activity in OA and CL studies (for related factor, see Nolde, Johnson, & Raye, 1998). (2) Regarding the ''age of memories,'' they tend to be more varied and remote in OA conditions (e.g., weeks, years, and decades) than in CL conditions (e.g., minutes, hours, or days). There is evidence that remoteness modulates the involvement of hippocampal regions during episodic retrieval (Maguire & Frith, 2003; Alvarez & Squire, 1994; however, see Nadel & Moscovitch, 1997), and thus, this factor could account for differences in the frequency of hippocampal activations in OA and CL studies. (3) The ''emotional content'' of memories tends to be greater and more varied in OA than in CL conditions, possibly accounting for amygdalar activations in some OA studies (e.g., Piefke, Weiss, Zilles, Markowitsch, & Fink, 2003; Fink et al., 1996). (4) Autobiographical conditions and laboratory conditions may also differ regarding ''retrieval success,'' that is, the amount of episodic information recovered in each scanned trial. Retrieval success is a critical factor because it has been shown to modulate activity in several brain areas, including the medial temporal lobe (MTL), PFC, parietal, and precuneus regions (Rugg & Henson, 2002; Cabeza & Nyberg, 2000). Retrieval success may differ between OA and CL studies but this difference is difficult to assess because most OA conditions do not permit measures of retrieval accuracy.

OA and CL conditions also tend to differ regarding self-referential processing, visual/spatial memory, and the amount of recollection/source memory during retrieval. (5) Although ''self-referential processing'' is a prerequisite for episodic memory retrieval (Tulving, 2002), it tends to be more pronounced in OA than in CL conditions. In OA conditions, the rememberer is usually an agent or an interested participant of the events retrieved, whereas in CL conditions, the rememberer is usually more passive, less implicated in the events retrieved, and has a similar relation to all items. Given that self-referential processing has been associated with medial PFC activity (Kelley et al., 2002; Gusnard, Akbudak, Shulman, & Raichle, 2001; Craik et al., 1999; Frith & Frith, 1999; Lane, Fink, Chau, & Dolan, 1997), this factor could account for the medial PFC activations found in some OA studies (Maguire, Henson, Mummery, & Frith, 2001; Maguire & Mummery, 1999; Andreasen, Paradiso, et al., 1999; Andreasen, O'Leary, et al., 1995). (6) Other conditions being equal, the ''visual/spatial memory'' is likely to be greater in OA than in CL conditions. In autobiographical conditions, memories are encoded in the rich and varied sensory environment of the real world, whereas in laboratory conditions, they are encoded in the impoverished and uniform environment of the laboratory. Differences in visual/spatial memory may be found in occipital (e.g., Wheeler, Petersen, & Buckner, 2000), parietal (e.g., Aguirre & D'Esposito, 1997; Owen, Milner, Petrides, & Evans, 1996a; Moscovitch, Kapur, Köhler, & Houle, 1995), and parahippocampal (e.g., Burgess, Maguire, Spiers, & O'Keefe, 2001; Cabeza, Rao, Wagner, Mayer, & Schacter, 2001; Owen, Milner, Petrides, & Evans, 1996b) cortices. (7) Finally, because of greater self-referential processing and sensory retrieval (which enhance the experience of ''reliving''), ''recollection'' is likely to be greater for autobiographical than for laboratory memories. Given that recollection has been associated with hippocampal activity (Yonelinas, 2002; Yonelinas, Hopfinger, Buonocore, Kroll, & Baynes, 2001; Eldridge, Knowlton, Furmanski, Bookheimer, & Engle, 2000), differences in this factor could also contribute to frequent hippocampal activations in OA studies. It is important to note, however, that the effects of several of the factors above—particularly the last two—may be detectable only when other factors are kept

constant. For example, recollection differences may be attenuated, or even reversed, when memories in the autobiographical condition are remote and those in the laboratory condition are recent.

The foregoing analyses have two main limitations. First, evidence about activation differences between OA and CL conditions is largely based on cross-study comparisons (e.g., Maguire, 2001) and very few studies have actually compared these conditions within participants (Nyberg, Forkstam, Petersson, Cabeza, & Ingvar, 2002; Conway, Turk et al., 1999; Fink et al., 1996). Second, given the large number of factors differing between OA and CL conditions, activation differences, both cross-study and within-participants, are very difficult to interpret. The problem is particularly serious because a factor known to affect activity in many brain regions, retrieval success, is usually not controlled in OA conditions. To address these problems, we compared brain activity in autobiographical and laboratory conditions within-participants, and employed an autobiographical condition that differed from the laboratory condition in a manageable number of factors and that allowed a measure of retrieval accuracy. We dubbed this novel condition ''controlled autobiographical'' (CA).

The paradigm we employed, called here the ''photo paradigm,'' is a novel adaptation to functional MRI (fMRI) of a technique previously used in behavioral research (Burt et al., 1995). In the present application of this paradigm, undergraduate students were provided with digital cameras, and during 10 days, they took photos in specified campus locations (CA photos). Then, they returned to the laboratory, and were shown photos taken in the same locations by other participants (CL photos). A few days later, they were scanned while recognizing CA and CL photos. The two types of photos were very similar (see Figure 1), and were counterbalanced across participants. Because CA and CL photos depicted the same locations and were very similar, distinguishing between them required the retrieval of specific contextual details (i.e., recollection) and could not be based on overall familiarity. An important feature of the photo paradigm is that it provides something missing in OA conditions: a measure of retrieval accuracy.

Using the photo paradigm, we were able to vary encoding context (laboratory vs. ''real world'') while keeping Factors 1–4 constant. (1) The proportion of production and monitoring processes in CA and CL conditions were approximately matched because the task was the same, stimuli were similar, and accuracy was assessed in both conditions. (2) The age of memories was approximately equated because they were recent in both conditions. Although CA encoding occurred a few days before CL encoding, this difference is small when compared to differences of months and years between typical OA and CL. (3) The emotional content of memories was similarly low in both conditions. (4) Finally, possible differences in retrieval success were controlled by including in the event-related fMRI analyses only CA and CL trials associated with correct recognition responses (''hits''). It is important to note that the photo paradigm controls for these four factors while preserving a fundamental difference between laboratory and autobiographical conditions: Recognizing CL photos involves memory for events experienced in the laboratory, whereas recognizing CA photos involves memory for events experienced in the ''real world'' as

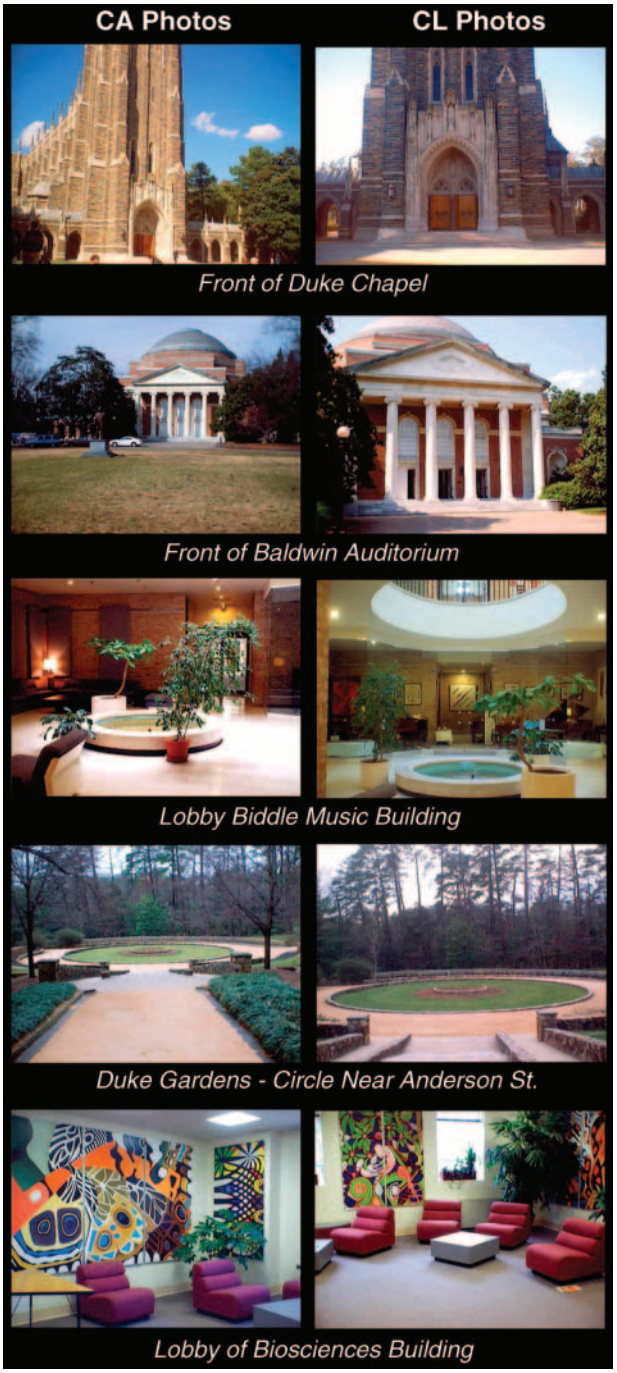

Figure 1. Examples of stimuli in CA and CL conditions.

part of the everyday life of the rememberer. Even though campus locations were specified, participants were encouraged to take the pictures in any order during their normal campus activities.

In contrast with Factors 1–4, Factors 5–7 differed between CA and CL conditions. (5) Self-referential processing can be assumed to be greater for CA than for CL photos. Whereas CA photos are taken by the rememberer, who makes personal decisions about the opportunity, orientation, and composition of the photos, CL photos are taken by someone else. (6) Visual/spatial memory can be assumed to be greater for CA photos, which were encoded in the rich three-dimensional environment of the real world, than for CL photos, which were viewed on the flat surface of a computer screen. (7) Finally, because of greater self-referential processing and visual/spatial memory, the CA condition is likely to involve greater recollection than the CL condition (Rubin, Schrauf, & Greenberg, 2003). Thus, we predicted that compared to the CL condition, the CA condition would yield greater activity in brain regions associated with self-referential processing (medial PFC), visual/spatial memory (occipital, parietal, and parahippocampal cortices), and recollection (hippocampus). At the same time, because both conditions assess episodic memory, we predicted activation overlaps in brain regions typically associated with episodic memory retrieval, including the PFC and MTL regions.

RESULTS

Behavioral Results

Corrected recognition scores (hits − false alarms) were 0.53 (0.70 − 0.17) for CA photos and 0.50 (0.57 − 0.07) for CL photos. The difference in corrected recognition scores was not significant ($p > .3$), suggesting that discriminability was similar for CA and for CL photos.

fMRI Results

Table 2 and Figure 2 show brain regions that were significantly activated in both CA and CL conditions (conjunction analysis), including the PFC, MTL, posterior parietal, anterior cingulate, and visual cortex regions. Visual cortex activations are consistent with the nature of the stimuli and the use of a fixation baseline. Common PFC activations for CA and CL were found in the right dorsolateral (see Figure 2B) and bilateral ventrolateral regions (see Figure 2C). Parietal activations were found posteriorly near the occipital boundary (see Figure 2D). As illustrated by the time courses in Figure 2, the latency and strength of PFC, parietal, and anterior cingulate activations was almost identical in CA and CL conditions. Finally, common MTL activations for CA and CL were also found bilaterally. These activations extended into the hippocampal formation, which as described below showed greater activity for CA than for CL. Thus, these activations are depicted in Figure 3, together with other regions showing CA–CL differences.

Table 3 and Figure 3 show regions that were significantly more activated for CA than for CL. No brain region was reliably more activated for CL than for CA after the FDR correction. Consistent with our predictions, regions differentially more involved in CA than in CL were found in the medial PFC, visual and parahippocampal regions, and the hippocampal formation. As indicated by the time course in Figure 3A, the medial PFC difference occurred because this region was ''less deactivated''

Table 2. Brain Regions Activated during Both CA and CL Conditions (Conjunction Analysis)

		Talairach Coordinates			*T score*	*T score*
Brain Region	*BA*	*x*	*y*	*z*	*CA*	*CL*
Right dorsolateral PFC	46	49	27	16	7.7	7.5
Bilateral ventrolateral PFC	47	34	29	−5	9.0	6.4
	47	−34	26	−5	8.2	7.7
Bilateral posterior parietal ctx.	39/19	−38	−83	22	8.5	10.2
	39/19	42	−81	18	9.3	9.3
Anterior cingulate	32	−4	17	44	7.8	6.4
Bilateral visual cortex	18/17	−4	−82	1	15.6	10.5
	19	11	−47	2	18.0	12.3
Bilateral hippocampal formation		−23	−27	−8	8.6	4.8
		23	−23	−6	7.1	5.1

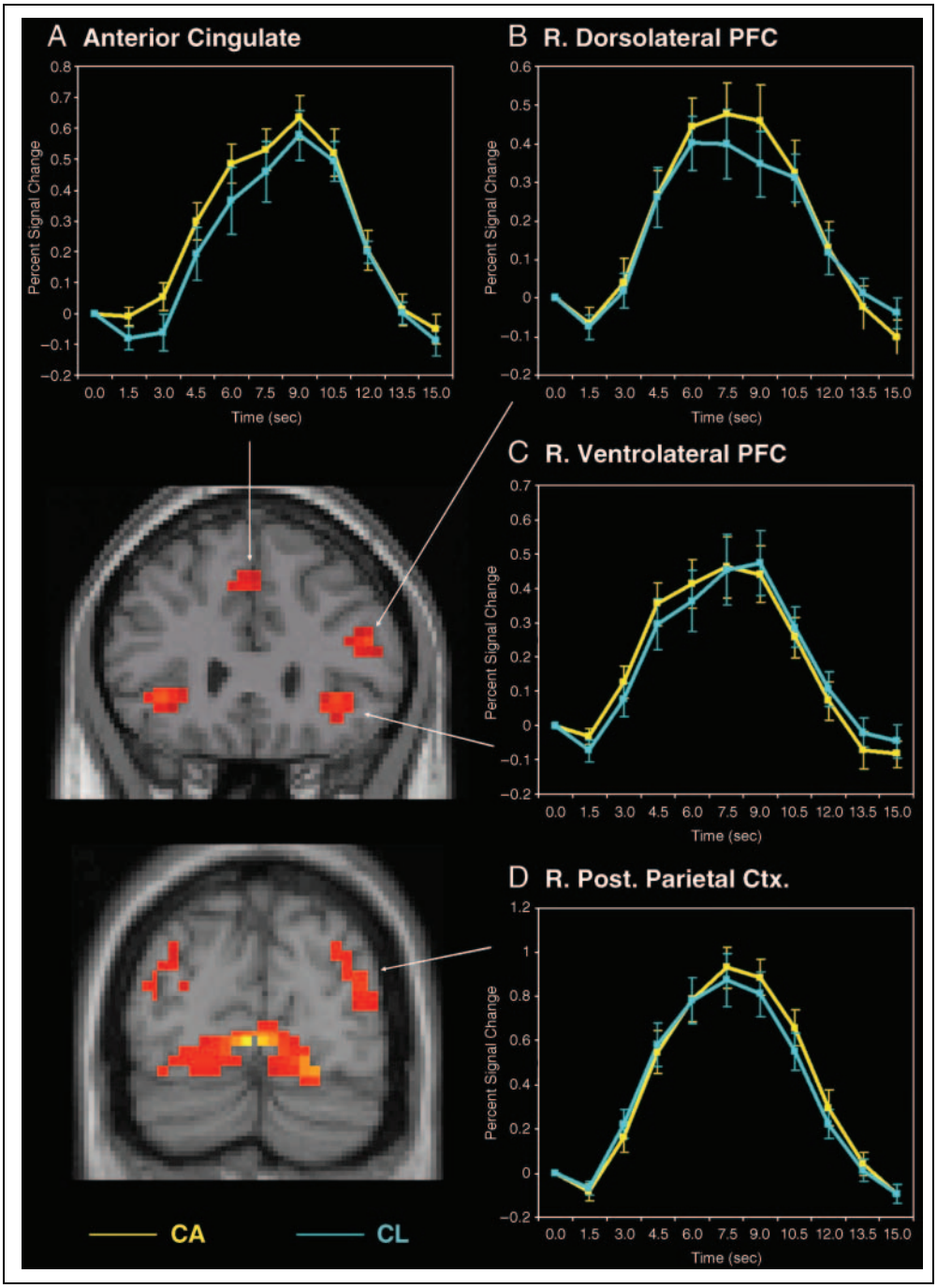

Figure 2. Brain regions activated during both CA and CL conditions (conjunction analysis). The time courses show percent signal change as a function of time (sec). (Ctx. = cortex; Post. = posterior; R. = right).

during CA than during CL. As discussed later, this is a typical pattern of activation difference in this region. Visual cortex activations were found in the left hemisphere, in the primary visual cortex within the calcarine fissure, and in the right hemisphere, in the cuneus region (see Figure 3B). The parahippocampal activation was right lateralized (see Figure 3C). Finally, greater activity for CA than for CL was also found bilaterally in the subiculum region of the hippocampal formation (see Figure 3D and E). Although these regions were significantly activated during both CA and CL (see above), they were more activated for CA than for CL. Confirming this idea, t tests on the data displayed in Figure 3D and E yielded significant differences in both the right ($p < .03$) and left ($p < .004$) hippocampal regions.

DISCUSSION

The results confirmed our predictions. First, CA and CL shared basic components of the episodic memory retrieval network, including the MTL and the PFC. Second, compared to CL, CA differentially recruited brain regions

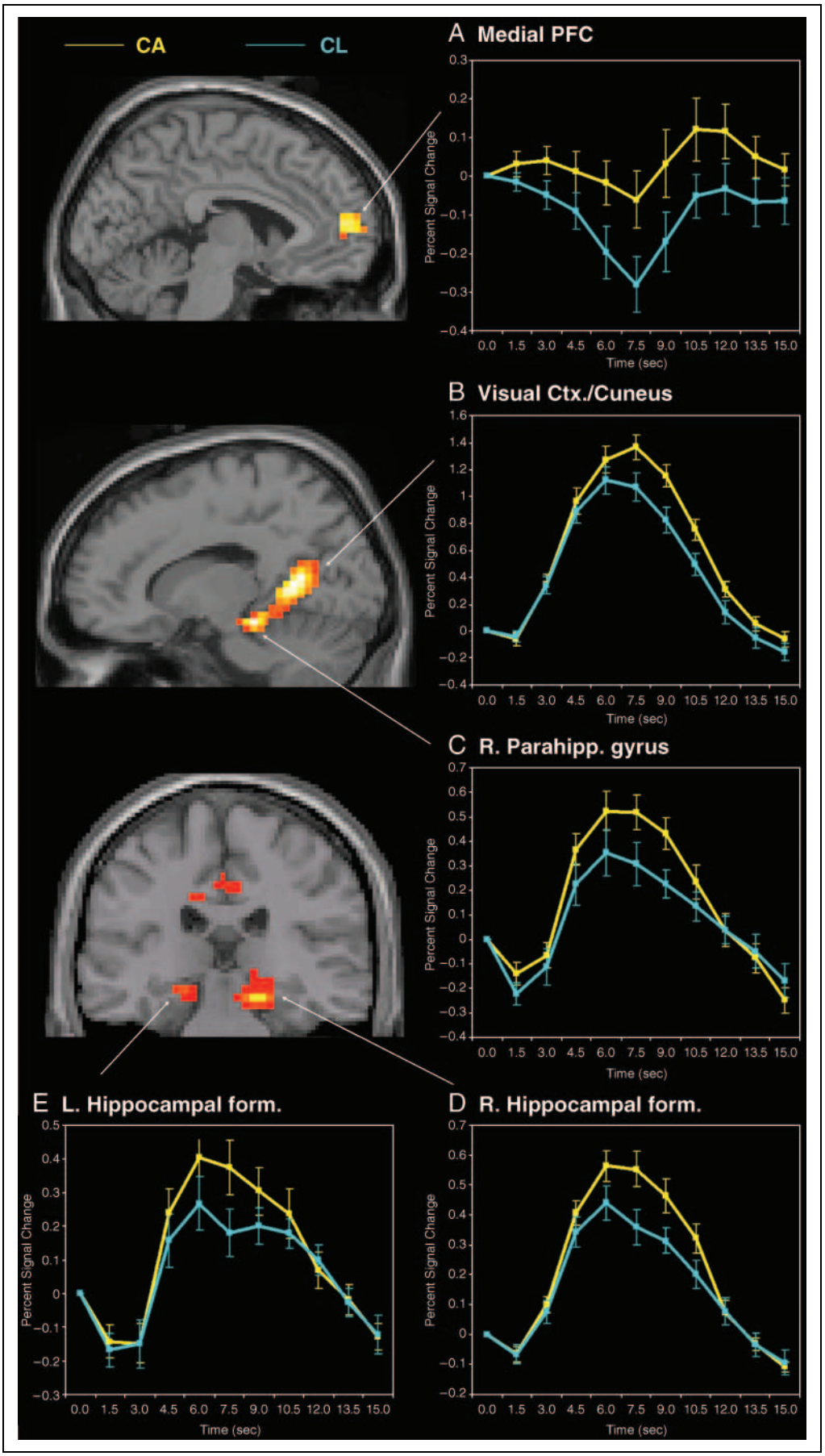

Figure 3. Brain regions showing greater activity in the CA condition than in the CL condition. The time courses show percent signal change as a function of time (sec). (Ctx. = cortex; Form. = formation; L. = left; Parahipp. = parahippocampal; Post. = posterior; R. = right).

Table 3. Brain Regions Showing Greater Activity during the CA Condition than during the CL Condition

		Talairach Coordinates			
Brain Region	*BA*	*x*	*y*	*z*	*T score*
Medial prefrontal cortex	10/32	−4	52	8	7.7
Visual cortex (primary, cuneus)	17/31	−15	−66	11	7.5
	31/30	15	−51	10	9.3
Right parahippocampal gyrus	35/36	15	−28	−15	9.1
Bilateral hippocampal formation		−23	−27	−8	4.0
		23	−29	−5	2.6

associated with self-referential processing (medial PFC), visual/spatial memory (visual and parahippocampal regions), and recollection (hippocampal formation). Below, we discuss these two groups of findings, and then mention some caveats.

Similarities between CA and CL Conditions

CA and CL shared regions typically associated with episodic memory retrieval, such as the MTL and the PFC (Cabeza & Nyberg, 2000). The overlap in the MTL is consistent with the assumption that CA and CL are mediated by the same MTL-dependent memory system (Squire, 1992). Shared activations were also found in the dorsolateral and ventrolateral PFC regions. As illustrated by Figure 2B and C, the time courses of these PFC activations were virtually identical for CA and CL. Given the presumed role of this region in retrieval control (Buckner & Wheeler, 2001; Moscovitch, 1992), the striking similarity of PFC activations suggests that—when the nature of retrieval cues and memory judgments is kept constant—retrieval strategies can be very similar in autobiographical and laboratory conditions. In contrast, if cues and memory judgments differ between CA and CL, differences in PFC activity are likely to occur. For example, two PET studies (Nyberg et al., 2002; Conway, Turk, et al., 1999) that compared an OA condition, in which participants generated autobiographical memories in response to cue words (Crovitz's Method), to a CL condition, in which they recalled word pairs before scanning, found greater left PFC activity for OA than for CL. This activation probably reflected greater production demands for OA than for CL, given that these control processes have been associated with left PFC activity (Cabeza, Locantore, et al., 2003; Wheeler & Buckner, 2003). In contrast, our study shows that when differences in the proportion of retrieval processes are kept constant, PFC regions are similarly involved in autobiographical and laboratory conditions.

Differences between CA and CL

Compared to the CL condition, the CA condition differentially engaged regions associated with self-referential processing (medial PFC), visual/spatial memory (occipital and parahippocampal regions), and recollection (hippocampal formation). Although self-referential processing plays a role in both autobiographical and laboratory memories (cf., semantic memory), it is particularly important for the former because autobiographical events are more relevant to the self than laboratory events. This difference is clear in the photo paradigm: Taking one's own photos involves active participation and selection, whereas viewing photos taken by others can be done passively, without much self-involvement. At retrieval, CA photos are likely to elicit memories of oneself taking the picture, making decisions, and so forth, whereas CL photos are less likely to elicit self-related information. In functional neuroimaging studies, self-referential processing has been associated with activations in the medial PFC, very close to the one found in the present study (Kelley et al., 2002; Gusnard et al., 2001; Craik et al., 1999; Lane et al., 1997). For example, this region is more activated when deciding if a trait adjective (e.g., ''polite'') applies to oneself than when deciding if it applies to someone else (Kelley et al., 2002; Craik et al., 1999), and when evaluating internal states than when evaluating stimulus properties (Gusnard et al., 2001; Lane et al., 1997). Although described as ''activations,'' these differences often occur because the medial PFC region is ''less deactivated'' in the self-referential condition than in control conditions (Kelley et al., 2002; Gusnard et al., 2001). As illustrated in Figure 3A, this is exactly what we found. One explanation of this phenomenon is that

self-referential processing is part of a ''default state'' of the brain (Gusnard et al., 2001; Gusnard & Raichle, 2001). In sum, the present results extend evidence regarding the role of self-referential processing in evaluation (Gusnard et al., 2001; Lane et al., 1997) and memory encoding (Kelley et al., 2002; Craik et al., 1999) to the domain of episodic memory retrieval by demonstrating greater involvement of the medial PFC in autobiographical than in laboratory conditions.

As expected, greater activity during CA than during CL was also found in regions associated with the retrieval of visual and spatial information. This finding was expected because the real world provides a richer source of visuospatial information than the laboratory environment—an obvious difference in the photo paradigm. Memory judgments may rely on the recovery of sensory information when such information is diagnostic (e.g., Johnson, Hashtroudi, & Lindsay, 1993). CA and CL photos are very similar (see Figure 1) and distinguishing between them required the retrieval of specific visuospatial details about the original events. For example, one may recognize a CA photo because of the sunlight illuminating the scene (visual memory) or the angle from which the photo was taken (spatial memory). In the present study, visual cortex activations included the primary visual cortex, which is often activated in visual imagery tasks (Kosslyn, Ganis, & Thompson, 2001), and the cuneus/retrosplenial region, which is frequently activated in autobiographical conditions (Maguire, 2001) and—like the precuneus region (Fletcher et al., 1995)—may be also involved in visual imagery. The important role of visual imagery in autobiographical memory (Greenberg & Rubin, in press; Rubin, 1998) is supported by evidence that visual cortex damage can impair autobiographical memory (Rubin & Greenberg, 1998) and that occipital scalp potentials are greater during the retrieval of real than fictitious autobiographical events (Conway, Pleydell-Pearce, Whitecross, & Sharpe, 2003). As for the parahippocampal activation, activations in these regions have been associated with processing of spatial information (parahippocampal place area, Epstein & Kanwisher, 1998), and the retrieval of the location information (Owen, Milner, Petrides, & Evans, 1996b). A recent fMRI study found parahippocampal activations while participants retrieved locations of a virtual town they navigated before scanning (Burgess et al., 2001). The present study extends evidence of the role of visual and parahippocampal regions in visual/spatial memory to the retrieval of information from real-life events. Given their association with spatial memory (e.g., Aguirre & D'Esposito, 1997; Owen, Milner, Petrides, & Evans, 1996a; Moscovitch et al., 1995), we also predicted greater lateral parietal activity for CA than for CL. However, as illustrated in Figure 2D, these regions were similarly activated in both conditions. A speculative explanation is that the role of parietal regions in spatial memory was masked by their general role in retrieval success (Rugg & Henson, 2002; Cabeza & Nyberg, 2000; Konishi, Wheeler, Donaldson, & Buckner, 2000).

Finally, hippocampal regions also showed greater activity during CA than during CL. These activations were found bilaterally, consistent with recent evidence that both left and right hippocampal regions are involved in autobiographical memory for recent events (Maguire & Frith, 2003). Greater hippocampal activity for CA than for CL was expected based on the assumption that CA would involve a more intense recollective experience than CL, and evidence that recollection is associated with hippocampal regions (Yonelinas, 2002; Yonelinas et al., 2001; Eldridge et al., 2000). It is important to note that greater recollection for CA than for CL can be expected only when several factors that modulate recollection are kept constant. In conditions in which autobiographical memories are remote or involve repeated events (e.g., having lunch in a campus cafeteria), they may involve less recollection that the retrieval of salient CL events. In contrast, when these factors are controlled, as in the photo paradigm, the autobiographical memories are likely to involve a more important recollective component because they involve greater self-referential processing and visuospatial imagery.

Caveats

A few cautionary notes are in order. First, the results of the present CA condition generalize to OA conditions in some dimensions but not in others. As listed in Table 1, our CA condition differed from typical OA conditions in terms of the proportion of retrieval processes, the age of memories, and emotional content. Thus, the present results should not be interpreted as suggesting that there are no differences between autobiographical and laboratory memories regarding the lateralization of the PFC (Nyberg et al., 2002; Conway, Turk et al., 1999) and hippocampal (Maguire, 2001) regions or the role of the amygdala (Piefke et al., 2003; Fink et al., 1996). These differences were not found in the present study because we kept retrieval processes, remoteness, and emotional content constant, not because these are not important features of autobiographical memory. On the other hand, the present results generalize to OA regarding self-referential processing, visual/spatial memory, and recollection.

Second, our CA and CL conditions are not ''pure'' measures of autobiographical and laboratory memory. Given that CA and CL photos were from the same locations, there is a chance that CA photos elicited some memories about the laboratory session and that CL photos elicited some memories about the photo-taking period. Although such potential ''contamination'' suggests one should be cautious when interpreting common activity for CA and CL, this issue is less serious in the case of differences in activation between these conditions. In the direct contrast between CA and CL,

common elements including possible contaminations tend to be subtracted out, and the resulting activations reflect mostly differences between the conditions.

Finally, although the task scanned was a source memory task, the critical findings are not about source memory processes. In the present study, participants decided whether familiar pictures were encoded in the campus or in the laboratory. In this sense, the present study resembles functional neuroimaging studies in which participants retrieve the perceptual (Cabeza, Locantore, et al., 2003; Ranganath, Johnson, & D'Esposito, 2000; Nolde, Johnson, & D'Esposito, 1998), spatial (Cansino, Maquet, Dolan, & Rugg, 2002; Rugg, Fletcher, Chua, & Dolan, 1999), or temporal (Cabeza, Locantore, et al., 2003; Cabeza, Mangels, et al., 1997) source associated with studied items. However, the goal of the present study was different than in typical source memory studies. In source memory studies, the critical comparison is between a source memory task and an item memory task, and activation differences between the various sources (e.g., left vs. right side of the screen) are usually not investigated because they are expected to be minimal. In the present study, in contrast, the critical comparison was between the two sources (campus vs. laboratory), and activity related to source memory in general was subtracted out because it was common to both sources. This explains why activity in brain regions strongly associated with source memory, such as the PFC, was common to CA and CL conditions and did not differ between them.

Conclusions

In summary, the present study identified similarities and differences between the neural correlates of episodic memory retrieval for autobiographical and laboratory events. Consistent with the notion that both forms of event memory depend on the same episodic or declarative memory system, the two conditions shared a network of regions that included the MTL and PFC regions. At the same time, the autobiographical condition elicited greater activity than the laboratory condition in brain regions associated with self-referential processing (medial PFC), visual/spatial memory (visual and parahippocampal regions), and recollection (hippocampal formation).

It is important to note that the reason why we found activations in these particular regions and not in others is because we manipulated self-referential processing, visual/spatial memory, and recollection, while keeping retrieval processes, memory remoteness, emotional content, and retrieval success constant. If, instead, for example, we had manipulated emotional content, we probably would have found differences in amygdalar activity (Piefke et al., 2003). Thus, the more general point we would like to make is that activation differences between autobiographical and laboratory studies can be explained without the need of postulating separate memory systems. Even if both types of conditions depend on the same episodic memory system, activation differences are likely to occur because of many factors that tend to differ between typical autobiographical and laboratory conditions. Thus, the best strategy to understand these activation differences is to manipulate some factors while keeping other factors constant. The photo paradigm provides a new way of achieving greater control over several of these factors.

METHODS

Subjects

The subjects were 13 Duke University students (10 women) with a mean age of 20.8 ($SD = 2.2$). They were healthy, right-handed, native English speakers, with no history of neurological or psychiatric episodes, and at the time of testing, they had been at university for a least one year. All subjects gave informed consent to a protocol approved by the Duke University Institutional Review Board.

Materials and Behavioral Procedures

The study consisted of three phases. During the first phase, which lasted about 10 days, participants took 120 photos of 40 campus locations (3 pictures per location). Several pictures per location were requested in order have enough trials for event-related fMRI analyses and to have spare photos in case some of them were of poor quality or too similar. The locations were well-known places within the Duke Campus (e.g., front of Duke Chapel), both indoors and outdoors (see examples in Figure 1). At the beginning of the study, participants visited the laboratory, where they received a digital camera (Intel Pocket PC Camera), a list of campus locations, and instructions on how to use the camera and take the photos. Participants were instructed to take pictures throughout the entire 10 days, trying not to visit more than four locations per day. They were told that the three photos of each location had to be different (e.g., from different views). Because the digital cameras employed do not have an LCD screen, participants had to use the viewfinder in order to take the pictures and could not review previous pictures. Moreover, they were instructed not to download the photos to a computer, and were not provided with the special USB A–B cable and camera-specific driver required for downloading. Participants were instructed to remember the taking of each picture as an individual event, and to do so by mentally noting the particular physical (light, temperature, etc.) and psychological (associations, mood) aspects of each picture-taking event. They were not allowed to take notes, or include any location name in their planners. To make sure participants could not

recognize their own photos without remembering the photo-taking event, they were instructed to always take the pictures in landscape format and during daylight hours, and never include familiar people (e.g., a friend) or objects (e.g., their backpack). Some photos were slightly edited with Photoshop to adjust brightness and contrast, and those inconsistent with the instructions were excluded. For each of the 40 locations, two of the three pictures were selected, thereby yielding a set of 80 ''CA photos.'' During the second phase, which occurred at the end of the 10-day photo-taking period, participants were shown on a computer monitor 80 photos (two per location) of the 120 CA photos of a different participant, who was randomly selected among previous fMRI or pilot participants while minimizing differences in weather-related elements displayed in the photos (e.g., snow on the ground). In the laboratory, each photograph was shown for 10 sec, and at the end of this period, subjects rated the aesthetic quality of the picture from 1 = ''very bad photo'' to 5 = ''excellent photo.'' The photos presented in the laboratory during the second phase of the study constituted the ''CL photos.'' During the third phase, which occurred 1 to 3 days after the second phase (mean 1.9 days), participants were scanned while recognizing CA photos and CL photos. Photographs of the same locations taken by other participants but not shown in the second phase were also included as distractors. For each photo, participants pressed a key to indicate if it was a photo they took, a photo they rated in the laboratory, or a new photo. Each photo was presented for 6 sec, followed by a response screen for 1.5 sec, and then by a fixation cross for a varying interval between 7.5 and 10.5 sec (total trial = 15–18 sec). Because participants were instructed to wait until the response screen appeared before making a response, reaction times are not informative and were not collected. The rationale for this procedure was to promote accuracy rather than speed, and to encourage attention to the recollective experience in both CA and CL conditions.

fMRI Methods

Scanning

Anatomical and functional MRI scanning was conducted using a 4-T GE magnet. Anatomical scanning started with a T1-weighted sagittal localizer series. The anterior (AC) and posterior commissures (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 450-msec repetition time (TR), a 9-msec echo time (TE), a 24-cm field of view (FOV), a 256^2 matrix, and a slice thickness of 1.9 mm. Functional scanning employed an inverse spiral sequence with a 1500-msec TR, a 6-msec TE, a 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 cubic 3.75 mm^3 isotropic voxels.

Analyses

Image preprocessing and analyses were performed using SPM99 (www.fil.ion.ucl.ac.uk/spm/). Functional images were corrected for acquisition order, and realigned to correct for motion artifacts. Anatomical images were coregistered with the first functional images for each subject, and then both anatomical and functional images were spatially normalized to a standard stereotactic space, using the templates implemented in SPM99. The coordinates were later converted to Talairach and Tournoux's (1988) space. Subsequently, the functional images were spatially smoothed using an 8-mm isotropic gaussian kernel, and were proportionally scaled to the whole-brain signal. For each subject, evoked hemodynamic responses to event types were modeled as box-car functions convolved with a synthetic hemodynamic response function. The general linear model, as implemented in SPM99, was used to model the effects of interest and other confounding effects (e.g., head movement and magnetic field drift). We assessed Statistical Parametric Maps (SPMs) for each individual subject by applying linear contrasts to the parameter estimates for the events of interest, resulting in a *t*-statistic for every voxel. Trials associated with correct and incorrect responses were modeled separately, and only the results of successful recognition of CA and CL photos (''hits'') are reported. Group averages were calculated for each condition by employing a one-sample *t* test (random effects analysis). To identify the general network of regions involved in autobiographical and laboratory memory, we contrasted CL and CL separately with the fixation baseline at a threshold corrected for false discovery rate (FDR) (Genovese, Lazar, & Nichols, 2002) of $p < .005$, using a minimum cluster size of five voxels. Next, in order to identify regions that were common to CA and CL conditions (i.e., a conjunction), the resulting T map image of the CA condition was inclusively masked with the T map image of the CL condition. The same threshold ($p < .005$; FDR-corrected; min. cluster size = 5) was applied to test for possible differences between CL and CA activity (i.e., the contrasts CA–CL, and CL–CA). Because we had a specific prediction for activation differences in the hippocampal formation, a less conservative threshold was used in this area ($p < .01$; uncorrected; min. cluster size = 5). For display purposes, the activations in the figures were thresholded at *p* values between .01 and .005. Using custom software from the ''Brain Imaging and Analysis Center'' (BIAC) of Duke University, the time courses of fMRI activations were assessed by averaging the mean raw MRI signal time-locked to the onsets of the different event types, and

converting it to percent signal change from the first image of the trial.

Acknowledgments

We thank Amber Baptiste for participant recruitment. This research was supported by the National Institute on Aging of the National Institutes of Health (AG19731 and AG023123).

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The data reported in this experiment have been deposited in the fMRI Data Center (http://www.fmridc.org). The accession number is 2-2004-116F5.

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