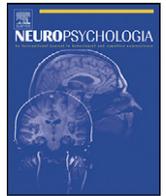




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Neural systems mediating field and observer memories

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ABSTRACT

Autobiographical memories are more imbued with affect when one adopts a first-person or field perspective during event retrieval, rather than a third-person or observer perspective. We combined fMRI, event narratives, and subjective ratings to identify the neural networks engaged with field versus observer memories for real-world events. Our results revealed significant decreases in bilateral insula and left somato-motor activity during the recall of observer memories, paired with a small relative increase in right posterior amygdala activity coincident with the recall of field memories. Notably, these regions showed no overlap with those areas mediating the narrative content and subjective emotionality of the remembered events. Our findings suggest that the emotionality of field relative to observer memories is not simply driven by increased limbic activation when one adopts a first-person retrieval perspective. Rather, there is also a significant reduction in one's cortical representations of the physical, embodied self when a third-person – or disembodied – perspective is taken at retrieval.

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1. Introduction

Events of the personal past are retrievable from two perspectives. One is through the rememberer's own eyes, as if he or she were looking outward, watching the events unfold anew. Alternatively, autobiographical memories may be recalled from a spectator's standpoint, which allows an individual to see him or herself as an actor in the memory image. These two modes of remembering are referred to as field and observer memories, respectively.

The distinction is important for several reasons. First, the fact that first-person perceptions can be transformed into third-person recollections reflects the active, reconstructive nature of autobiographical recall and refutes the idea that human memory works like a video camera that passively and veridically records perceptual experience for later playback (Loftus & Loftus, 1980; Nigro & Neisser, 1983). Second, the field/observer distinction underscores the unique capabilities of episodic memory—that “true marvel of nature” which Tulving (2002, p. 1) has brought into bold relief. Besides making it possible for people to reexperience their past and project themselves into the future, and thus travel mentally through subjective time (Tulving, 1983), episodic memory enables rememberers to navigate from either a participant's or an actor's point of view. Third, research reviewed by Schacter (1996, p. 22) leads to the “surprising, even startling observation that . . . the emotional intensity of a memory is determined, at least in part, by the way

in which you, the rememberer, go about remembering the episode. And the emotions that you attribute to the past may sometimes arise from the way in which you set out to retrieve the memory in the present.”

To amplify the last point, several studies have shown that, in comparison with observer memories, field memories are accompanied by more intense affect (Nigro & Neisser, 1983; Robinson & Swanson, 1993; Talarico, LaBar, & Rubin, 2004) and their narratives contain more information about “internal” aspects of the event, such as physical sensations and psychological motivations, but less information about “external” aspects, such as how things looked and where things were. These differences have been demonstrated in research on autobiographical memory for both innocuous incidents and traumatic events, such as shooting a basketball versus being struck with a baseball bat (McIsaac & Eich, 2002, 2004; Robinson, 1996).

Though earlier experiments have established a connection between retrieval perspective and event emotionality, how this relation is mediated in the brain remains unknown. Here we combined fMRI, event narratives, and subjective ratings in a novel attempt to isolate the neural systems engaged with field versus observer memories for complex, naturalistic events.

At least two systems are apt to be involved. On the one hand, not only is the amygdala integral to emotion-related effects on memory encoding and consolidation (Dolcos, LaBar, & Cabeza, 2004; Hamann, Eit, Grafton, & Kilts, 1999; Kensinger & Schacter, 2006; McGaugh, 2004; Phelps, 2004; Richardson, Strange, & Dolan, 2004), but also, recent evidence suggests that the amygdala also plays a central role in the retrieval of emotional memories (Cabeza &

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St. Jacques, 2007; Daselaar et al., 2008; Dolcos, LaBar, & Cabeza, 2005; Fink et al., 1996; Greenberg et al., 2005; LaBar, 2007; Smith, Dolan, & Rugg, 2004). On the other hand, awareness of one's on-going subjective emotional states is inextricably linked to the conscious monitoring of one's on-going visceral, physiological states (Damasio, 1994), an idea traceable to James (1884) over a century ago. Critical to this interoceptive ability are the insula and somatosensory cortices (Critchley, Wiens, Rothstein, Öhman, & Dolan, 2004; Damasio et al., 2000; Pollatos, Gramann, & Schandry, 2006). Given that visual-perceptual aspects of memory retrieval rely on the same cortical systems used when actually perceiving a stimulus (e.g., Handy et al., 2004; Wheeler, Petersen, & Buckner, 2000; see Cabeza & St. Jacques, 2007), we hypothesized that either or both of these emotion-related systems might show a similar reactivation in response to autobiographical memory retrieval. Accordingly, the primary aim of our study was to test the prediction of a greater response in the amygdala, insula, and somatosensory regions for field relative to observer memories.

We also had a secondary, control-related aim. In particular, the recall of complex autobiographical memories unconstrained for field versus observer perspective has been linked to an extensive network of brain regions, including left ventral, dorsal, and medial prefrontal cortices, medial temporal areas, and the inferior parietal lobule (Cabeza & St. Jacques, 2007; Maguire, 2001; Schacter, Addis, & Buckner, 2007). Critically, however, brain regions engaged during memory retrieval are not limited to those associated with the act of retrieval itself. In addition, the subjective experience of the retrieved memory will also influence the pattern of activation obtained. This introduces a source of variance in fMRI data that is associated with the phenomenological attributes of the event being recalled, rather than with the retrieval network itself (Addis, Wong, & Schacter, 2007). Thus the secondary aim of our study was to identify any brain regions that correlate positively with phenomenological differences between field and observer memories, as reflected in either recall narratives or subjective ratings, in order to dissociate retrieval networks per se from those regions that simply vary with the subjective experience of remembering, independent of the specific mode of retrieval.

2. Methods

2.1. Overview

The experiment took place over two days for each participant. On the first day, university students completed four complex, physical tasks, such as creating an original work of art and taking a roundabout walk across campus. One week later, participants were scanned as they silently recalled each task twice: the first time from either the field or observer perspective, and the second time from either the same perspective as on the initial recall occasion (field/field vs. observer/observer conditions) or from the contrasting vantage point (field/observer vs. observer/field).

Our fMRI paradigm was based on a blocked design having interleaved epochs of silent task recall and a visual-search task used as a cognitively active baseline condition. Participants were visually cued at the start of each recall block to silently remember a particular task (the art project, for instance) from a particular perspective (field or observer); the task and perspective remained constant for all recall blocks in a given functional run. To obtain measures of memory content, at the end of each run participants verbalized the thoughts and images they had experienced during the task-recall epochs; their narratives were recorded on digital tape for later transcription and content analysis. To obtain measures of phenomenological experience, participants also rated the emotionality of their task-related recollections, how well they had maintained the designated perspective during retrieval, and how closely their verbal reports matched the recollections they had experienced during scanning.

2.2. Participants

Study participants included 16 university students (7 men and 9 women) averaging 22.8 years of age (range 20–26). Informed consent was obtained in accordance with the standards and practices of the University of British Columbia (UBC) and our research methods were vetted and approved by the university's Clinical Research Ethics Board.

2.3. First-session testing

Participants were told that the study dealt with everyday cognition and that it would be divided into two sessions, spaced one week apart. During the first session, participants performed four fairly elaborate and physically engaging tasks, each lasting about 15 min. The tasks were carried out in and around the UBC Psychology Department and their order of completion was varied systematically across participants. The tasks required participants to:

- Create an original work of *art*, using the materials provided to them (mosaic tiles, colored piping, modeling clay, etc.).
- Make themselves lunch and *dessert*, using an assortment of ingredients (breads, fruits, deli meats, condiments, parfaits, etc.) that were placed before them on a counter. Drinks, utensils, and other supplies were also provided, and participants sat at the counter to eat their meal.
- Play a *game* of Torx: a hand-held, molded-plastic toy with moveable arms, joints, and handles. The device emitted a volley of voice commands (turn this, twist that) that had to be followed promptly, lest the game reset from the beginning. The game was entertaining for some participants, exasperating for others, exciting and challenging for all.
- Following a map, take a circuitous *walk* to and from a landmark building across campus.

2.4. Second-session testing

At the start of the second session, which was held in the UBC High-Field Neuroimaging Centre, participants were introduced to the distinction between field and observer modes of remembering and they practiced recalling their own high-school graduation from both perspectives. This was explained as preparation for the current scanning session, in which participants would be asked to adopt and maintain one perspective or the other as they recalled the tasks they had performed the week before. In addition, participants were familiarized with icons that would later be displayed, in the scanner, as cues to recall a particular task from a particular perspective (Fig. 1A and B). They were also briefed on a visual-search task that they would perform that was interleaved with the recall task, as part of our blocked fMRI design (Fig. 1C; see below). The search task was employed during these intervening blocks in order to maintain active cognitive engagement during the entire functional run, thereby mitigating concerns that increases in BOLD response during recall blocks could be attributed to a general increase in cognitive activity and/or arousal rather than to memory retrieval itself.

Our fMRI paradigm was based on a block-related design, such that changes in hemodynamic activity during the recall of the behavioral tasks were measured relative to hemodynamic activity during the visual-search task. Participants were scanned in eight separate functional runs. Each run consisted of alternating blocks of task recall (with the task being recalled and the visual perspective of retrieval held constant for the run) and visual-search, during which the participants remained silent as fMRI data were acquired continuously (Fig. 1D). After the completion of each functional run, participants described aloud the recollections they had experienced in the four preceding blocks of task recall. In the final phase of each run, participants rated the emotionality and other attributes of their recollections. These verbalized ratings, like the recollections themselves, were digitally recorded for later transcription and analysis.

Each functional run began with 20 s of a blank screen, followed by a pair of icons, presented for 2 s, that indicated (a) which of the four tasks was to be recalled and (b) which of the two perspectives (field or observer) was to be used. The display and timing of these and all other test stimuli were controlled by a personal computer running Presentation software (Neurobehavioral Systems, San Francisco, CA). The icons were followed by a blank screen for 22 s, during which participants silently recalled the specified task from the specified perspective (Fig. 1C and D).

The memory retrieval block ended and the visual-search block began with a single English letter of a particular color being presented at fixation that signaled the target for the upcoming search display, in terms of both the letter and its color (e.g., a red "Q"). Following a 2-s blank screen, the search display was presented for 14 s, followed first by a blank interval, and then by a number and question mark (e.g., "5?"). Participants then made a yes/no decision on whether this was the number of targets they had found in the search display (Fig. 1D). Across all repetitions of the visual-search procedure, the queried target number ("5?") matched the actual number of targets on only 50% of the search displays, and thus was not predictive of the correct answer. A 2-s blank interval followed the query, during which participants answered by pressing a yes or no button on a fiber-optic, MR-compatible response device (Lightwave Medical, Vancouver, BC).

In each functional run, participants alternated two more times between silent task-recall and visual-search procedures, with the designated task and perspective remaining the same across all blocks in the given run. This same silent recall task was then performed a fourth and final time, followed by a 20-s interval where the screen simply said "rest." In this manner, each functional run included four repetitions of memory testing (task recall) and three repetitions of control testing (visual-search).

Following the 20 s rest period, fMRI data acquisition was adjourned to allow participants time (about 2 min) to articulate their task recollections and to answer three questions:

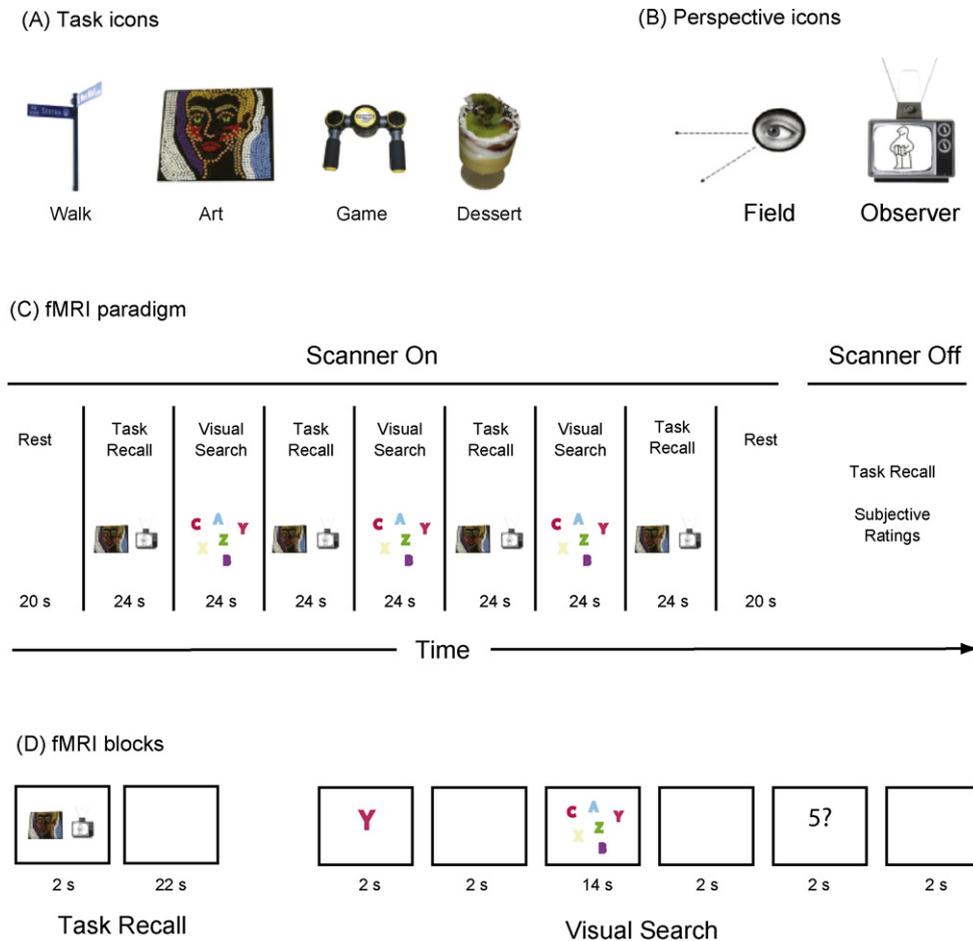


Fig. 1. Task (A) and perspective (B) icons used as condition cues during fMRI scanning. All participants were familiarized with these icons and how they related to the different task and perspective conditions prior to entering the scanner. (C) The timing of memory and control (visual-search) blocks during each fMRI scanning run. For task recall, the task and perspective remained constant for the entire scanner run. (D) The timing of events within each 24 s task recall (left) and visual-search/control (right) block.

- How consistently did you maintain the specified perspective (field or observer) during the preceding blocks of task recall?
- How emotional were your recollections?
- How closely did your verbal reports match what you were thinking about while the scanner was running during the task-recall blocks?

Participants answered these questions aloud with reference to a 1–5 (low–high) scale. Following this, the next of the eight functional runs began. For each participant, the functional runs were configured so that each of the four tasks was recalled twice, either from the same perspective – field (F) or observer (O) – on both occasions (conditions F/F and O/O) or from different perspectives (conditions F/O and O/F). The assignment of tasks and perspectives to functional runs and their order were counterbalanced across participants.

2.5. fMRI acquisition and analysis

Functional MRI data were collected on a research-dedicated Phillips 3-T Achieva scanner fitted with a SENSE head coil. A conventional spin-echo, T1-weighted sagittal localizer was used to view the positioning of the subject's head and to set the functional image volumes to be acquired in the AC–PC plane. Functional image volumes were collected with an EPI gradient echo pulse sequence (TR=2000 ms, TE=30 ms, 90° flip angle, FOV 240 mm × 240 mm, 128 × 128 matrix, 62.5 kHz bandwidth, 3.00 mm × 3.00 mm measured in-plane resolution, 3.00 mm slice thickness, 1.00 mm slice gap, 36 interleaved transverse slices). A high-resolution, T1-weighted structural image was acquired for each subject using a 3D gradient echo pulse sequence (TR=shortest, TE=shortest, 8° flip angle, FOV 256 mm × 256 mm, 256 × 256 matrix, 1.00 mm × 1.00 mm in-plane resolution, 1.00 mm slice thickness, 170 slices). Functional images were reconstructed off-line. Statistical Parametric Mapping software (SPM2, Wellcome Institute of Cognitive Neurology, London, UK) was used for motion correction, spatial normalization into MNI coordinates, and spatial smoothing with an 8 mm Gaussian kernel.

Single-subject statistical analysis was based on a multiple regression using the general linear model as implemented in SPM2. Task-recall and visual-search blocks in each functional run were modeled using a box-car reference waveform that was

convolved with the hemodynamic response function (HRF). Voxel-wise parameter estimates (β s) were then calculated within each run in order to quantify the degree to which the BOLD signal approximated the convolved HRF reference waveform; linear, quadratic, and cubic regressors were included in the regression model as effects of non-interest. All subsequent group-level analyses were based on random-effects models. One-sample *t*-tests were used for identifying voxel clusters showing significant increases in the BOLD response for field and observer memories, respectively, as well as areas showing relative increases with one recall perspective relative to the other.

Simple linear regression implemented in SPM2 was used to identify voxel clusters showing positive correlations with the behavioral measures predictive of either field or observer memories. All correlations performed were based on subtraction scores. For the behavioral measures, those predictive of field memories were based on subtracting for each subject their value of that measure in the observer condition from the corresponding value in the field condition, with the reverse subtraction used for those variables predictive of observer memories; all of these subtraction scores were then mean normalized. These mean-normalized difference scores were then correlated with the corresponding difference scores based on the voxel-wise β values for field and observer memories: difference scores predictive of field memories were correlated with the β value from the observer condition subtracted from the β value from the field condition, and vice versa for the mean-normalized variable difference scores predictive of observer memories. To compute the *r* values reported for each cluster in Tables 5 and 6, the relevant variable mean-normalized difference score was correlated using SPSS software with each participants' corresponding mean β difference value averaged across all voxels in the group-identified cluster.

Reported mean β values shown in Fig. 4 and Table 4, as well as the mean β values used in the regressions reported in Figs. 5 and 6, were derived using the MarsBaR region of interest toolbox for SPM (<http://marsbar.sourceforge.net/>) and custom MATLAB scripts. For all reported cluster coordinates across all conditions and analyses, transformation of MNI into Talairach coordinates was performed using a modified version of the mni2tal MATLAB script (<http://www2.bc.edu/~slotnics/scripts/mni2tal.m>).

Table 1
Behavioral measures of field and observer memories. (A) Mean ratings of various aspects of the participants' recollective experience, made on five-point scales. (B) Mean statements representing various content categories, per 100 words of recall narrative. (C) Mean internal and external memory contents, per 100 words of recall narrative. The former measure includes statements representing affective reactions, physical sensations, psychological states, and first-person accounts, whereas the latter measure includes statements indicative of physical actions, self-observations, and third-person accounts. Standard errors are enclosed in parentheses. The result column indicates differences between field and observer memories that were significant at an alpha of 0.01 (uncorrected comparisons in (A) and (C); Bonferroni-corrected multiple comparisons in (B)).

Behavioral measure	Field memories	Observer memories	Result
(A) Subjective ratings			
Perspective maintenance	4.68 (0.08)	3.77 (0.12)	F > O
Emotionality	3.44 (0.19)	2.20 (0.13)	F > O
Recollection/verbalization match	4.34 (0.12)	4.19 (0.08)	
(B) Narrative statements			
Affective reactions	1.34 (0.20)	0.14 (0.07)	F > O
Physical sensations	0.80 (0.17)	0.17 (0.06)	F > O
Psychological states	2.23 (0.35)	0.32 (0.11)	F > O
First-person accounts	9.46 (0.71)	5.90 (0.74)	F > O
Physical actions	4.13 (0.55)	7.65 (0.66)	O > F
Self-observations	0.13 (0.07)	2.43 (0.36)	O > F
Third-person accounts	0.15 (0.05)	2.22 (0.91)	O > F
Associated ideas	0.23 (0.07)	0.05 (0.05)	
Perceptual details	2.78 (0.30)	3.30 (0.33)	
Spatial relations	0.16 (0.05)	0.28 (0.09)	
(C) Memory contents			
Internal	13.83 (0.84)	6.53 (0.72)	F > O
External	4.41 (0.54)	12.30 (0.85)	O > F

3. Results

3.1. Subjective ratings

Data summarized in Table 1A show that although the participants were adept at maintaining the observer perspective during task recall (mean rating = 3.77 on a 1–5 scale), they found it even easier to maintain the field perspective (mean = 4.68; $F(1/15) = 16.30, p < 0.01$). This was true the first time they recalled a given task as well as the second time ($ps > 0.10$ for both the main effect of Recall Occasion and the Recall Occasion \times Recall Perspective interaction). There was also a significant advantage of field over observer memories in subjective ratings of emotionality (means = 3.44 vs. 2.20; $F(1/15) = 25.12, p < 0.01$), which again was independent of Recall Occasion, either alone or in conjunction with Recall Perspective ($ps > 0.10$). There were no significant differences between Recall Perspectives, Recall Occasions, or their interaction in terms of the closeness with which the participants' verbal reports matched the recollections they had silently experienced during scanning ($ps > 0.10$).

3.2. Recall narratives

A verbatim transcript was prepared of every subject's digitally recorded recall narratives and the total number of words produced was calculated by computer program. On average, transcripts for field memories were longer than those for observer memories (means = 150.2 vs. 110.2 words; $F(1/15) = 29.60, p < 0.01$). A non-significant trend in the same direction was seen in a previous study on memory for physically engaging but non-traumatic events (McIsaac & Eich, 2004).

Each transcript was coded according to 10 content categories that were defined in terms of narrative statements (single words or phrases) reflecting:

- Affective reactions (e.g., it was fun making the mosaic; I felt very happy and alert).
- Physical sensations from any sensory modality (e.g., the modeling clay felt soft; the parfait tasted sweet).
- Psychological states (e.g., I wondered how long my walk was taking; I was confused by some of the game's instructions).
- First-person accounts (e.g., I, me, mine).
- Physical actions (e.g., I sat down at the counter; I walked out the door).
- Self-observations (e.g., I can see myself running up the stairs; I seem to be looking over my own shoulder).
- Third-person accounts (e.g., he, they, Joanne walked into the room).
- Associated ideas, including knowledge or experiences acquired outside the current experimental content (e.g., my brother likes lemon pie and the dessert task made me think of him; playing with the mosaics reminded me of my childhood).
- Perceptual details, including descriptions of the task objects, including color, shape, size, and numerical quantifiers (e.g., the clay was teal blue; there were at least three kinds of bread) as well as descriptions of the environment that were not central to the tasks at hand (e.g., there were lots of old textbooks on the shelf; the sky was filled with billowy clouds).
- Spatial relations between objects and/or people (the sink was to the right of the fridge; Helen stood in front of the flagpole).

Coding of the transcripts was carried out by two research assistants, both blind to recall condition and study hypotheses. The assistants worked independently at first, using a coding guide or template that contained numerous examples (including those given above). The assistants met later to discuss and resolve any coding differences between them, which were usually small (a discrepancy of one or two statements in any given content category).

For each subject, the number of statements in each category was divided by the total word length of his or her transcript, and the resulting quotients were multiplied by 100 (to control for the aforementioned difference in transcript length between field and observer memories). The data were then averaged over participants to yield the mean frequencies shown in Table 1B.

Multivariate analysis of variance was performed using Recall Perspective (field vs. observer), Recall Occasion (first vs. second), Task Number (first vs. second task recalled from a given perspective), and the 10 aforementioned varieties of Narrative Statements as the variables. The main effect of the latter variable was significant (univariate $F(9/135) = 77.31, p < 0.01$; multivariate Wilks' $\lambda(9/7) = 82.28, p < 0.01$). Also significant, and of greater importance, was the interaction between Narrative Statements and Recall Perspective (univariate $F(9/135) = 13.62, p < 0.01$; multivariate Wilks' $\lambda(9/7) = 9.19, p < 0.01$). Supplemental comparisons, using a Bonferroni-adjusted alpha of 0.01 (i.e., 0.10/10), revealed significantly more statements representing affective reactions, physical sensations, psychological states, and first-person accounts with field memories, and significantly more reports of physical actions, self-observations, and third-person accounts with observer memories. No other effects, simple or interactive in nature, were significant ($ps > 0.05$), which suggests that these differences were constant over Recall Occasions and independent of Task Number.

To simplify correlational analyses of brain/behavior relations, described below, we generated two global measures of memory content (Table 1C). One of these measures, internal memory content, was created by combining the mean number of statements (per 100 words of recall narrative) that were predictive of field memories (viz. affective reactions, physical sensations, psychological states, and first-person accounts, as shown in Table 1B). The other measure, external memory content, was created by adding together the mean number of statements (again, per 100 words of

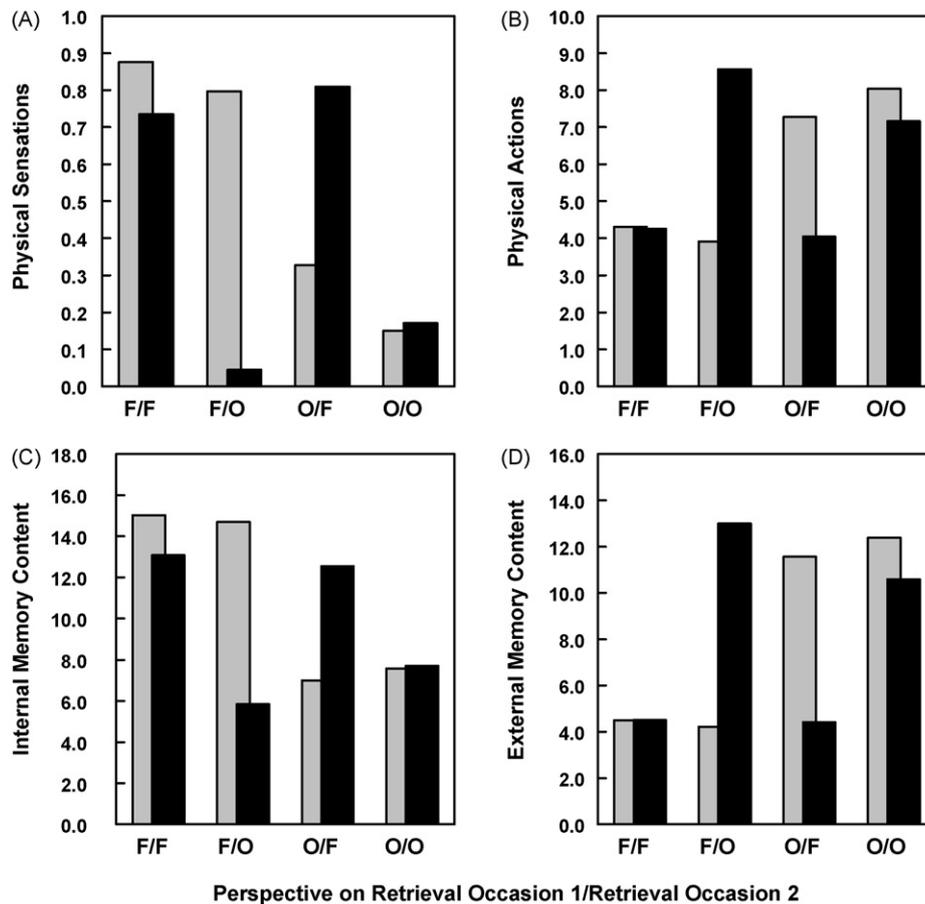


Fig. 2. Representative differences in the narrative contents of field (F) and observer (O) memories. Asked to recall complex tasks they had completed one week earlier, participants mentioned more of the physical sensations they had experienced (A), but fewer of the physical actions they had performed (B), when in the field as opposed to the observer mode of remembering. More generally, field narratives outscored observer narratives representing internal memory content—that is, physical sensations, affective reactions, psychological states, and first-person accounts, which are added together in (C). In contrast, observer narratives included comparatively more statements reflecting external memory content—that is, physical actions, self-observations, and third-person accounts, which are combined in (D). In all cases, content differences between field and observer memories were equally robust on the first and second retrieval occasions (light and dark bars, respectively).

recall narrative) that were predictive of observer memories (viz. physical actions, self-observations, and third-person accounts, also as shown in Table 1B).

Both measures were calculated for every subject, and the resulting scores were analyzed in the context of $2 \times 2 \times 2$ design (Recall Perspective \times Recall Occasion \times Task Number). Predictably, analysis of the internal content data demonstrated a significant advantage of field over observer memories ($F(1/15) = 41.04, p < 0.01$), while analysis of the external content results revealed a reliable difference in the opposite direction ($F(1/15) = 70.33, p < 0.01$). In neither instance did the difference between Recall Perspectives vary as a function of Recall Occasion, Task Number, or any interaction involving these variables.

To recap, the behavioral results of this study replicate prior reports (McIsaac & Eich, 2002, 2004) in showing that participants rated their field memories as being more emotionally charged than their observer memories (Table 1A). In addition to affecting the subjective experience of remembering, recall perspective influenced the content of the participants' recollections in several respects (Table 1B). Relative to observer memories, recollections narrated from the field perspective contained more statements about the affective reactions, physical sensations, and psychological states that participants experienced during task performance, as well as more frequent use of first-person pronouns to describe these experiences. In contrast, narratives of observer memories contained comparatively more statements involving physical actions, self-observations, and third-person accounts. Thus, whereas field

memories were relatively rich in “internal” content, observer memories held a comparative advantage in “external” content (Table 1C). These perspective-dependent differences in memory content were evident the first time the tasks were recalled and they re-emerged with comparable clarity on the second recall occasion (Fig. 2A–D).

3.3. Imaging data

As noted above, our paradigm was based on a blocked design such that changes in hemodynamic activity during memory recall were measured relative to the visual-search control task. Analysis of the block-related fMRI data itself proceeded in a three-step sequence. The first step was to identify those brain regions showing significant increases in the blood-oxygenation level dependent (BOLD) signal during recall from the field and observer perspectives, respectively. For field memories, regions of increased BOLD activity relative to the visual-search task baseline included left prefrontal cortex (PFC) extending through dorsomedial, dorsolateral, ventrolateral, and ventromedial portions, the angular gyrus bilaterally, the hippocampus bilaterally, the left amygdala, and precuneus (Fig. 3A and Table 2). For observer memories, regions of increased BOLD activity relative to the visual-search task baseline also included left PFC extending through dorsomedial, dorsolateral, ventrolateral, and ventromedial portions, along with the angular gyrus bilaterally, the hippocampus bilaterally, and the precuneus (Fig. 3B and Table 3). Notably, these loci of activation paralleled the network of regions previously implicated in the recall of complex auto-

Autobiographical Memory Retrieval

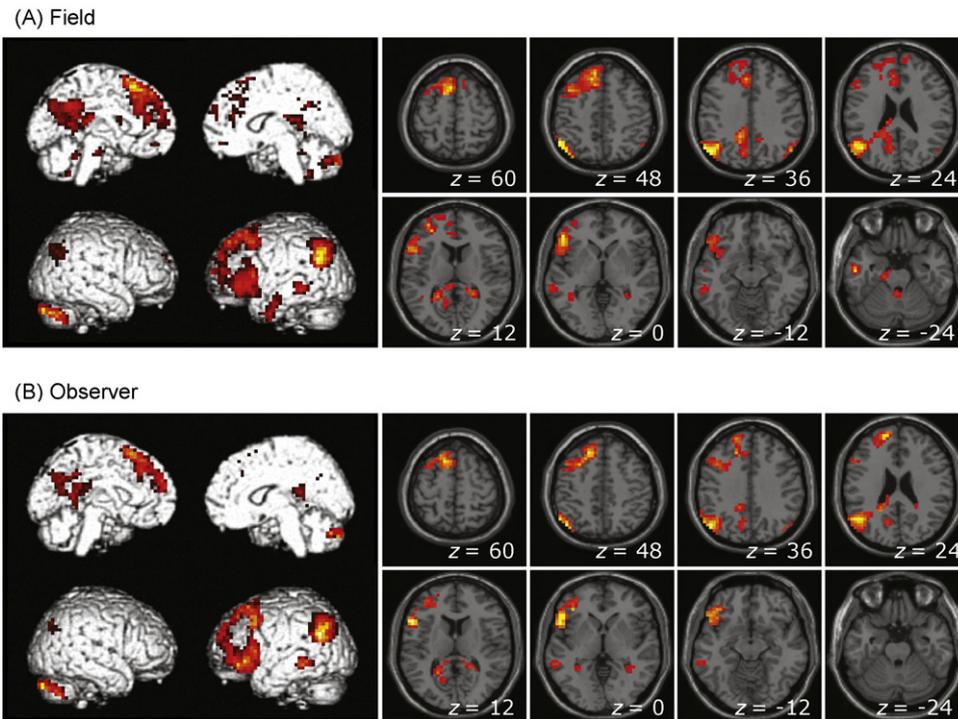


Fig. 3. Autobiographical memory retrieval. Rendered and anatomical images showing areas increasing in hemodynamic activity for (A) field and (B) observer memories. Common to both retrieval conditions were responses in right prefrontal cortex, bilateral inferior parietal lobule, and bilateral medial temporal cortex. All data are based on a threshold of $p < 0.001$ (uncorrected); clusters are shown on the MNI anatomical template provided with SPM2.

Table 2
 Clusters showing significantly increased BOLD response for field memories. Reported statistics are based on a threshold of $p < 0.001$ (uncorrected) and a minimum cluster size of $k \geq 10$ contiguous voxels. Reported coordinates are for the cluster maxima, as defined by t -value; for clusters with multiple coordinates, local maxima are also reported. BA, Brodmann's area.

Hemi	Structure	Area	k	t	MNI coordinates			Talairach coordinates		
					X	Y	Z	X	Y	Z
Frontal										
Left	Superior frontal gyrus	BA 8	875	11.86	-12	24	52	-12	26	47
	Middle frontal gyrus	BA 47		9.65	-48	36	-4	-48	35	-5
	Inferior frontal gyrus	BA 45		9.27	-48	28	4	-48	27	2
Right	Superior frontal gyrus	BA 9	16	5.08	12	56	28	12	56	23
Temporal										
Left	Middle temporal gyrus	BA 21	62	8.15	-52	-12	-24	-51	-13	-20
	Inferior temporal gyrus	BA 20		7.86	-44	-8	-36	-44	-9	-30
	Middle temporal gyrus	BA 21	49	6.83	-60	-44	-8	-59	-43	-5
Right	Precuneus	BA 31	11	5.07	12	-52	32	12	-49	32
Temporal-parietal										
Left	Middle temporal gyrus	BA 39	543	11.00	-44	-64	28	-44	-61	29
	Inferior parietal lobule	BA 40		10.45	-52	-56	48	-51	-52	47
	Angular gyrus	BA 39		10.44	-56	-64	36	-55	-60	36
Right	Angular gyrus	BA 39	33	6.95	52	-68	36	51	-64	36
				5.73	48	-76	32	48	-72	33
	Inferior parietal lobule	BA 40		5.48	56	-60	40	55	-56	40
Cerebellum										
Right	Anterior lobe	-	13	5.40	0	-44	-24	0	-44	-18
	Posterior lobe	Tuber	177	9.23	44	-68	-36	44	-67	-27
		Uvula		8.73	28	-84	-36	28	-83	-26
				8.16	20	-88	-36	20	-87	-26
				11	7.44	4	-52	-48	4	-52
Limbic										
Left	Parahippocampal gyrus	BA 19	16	5.07	-36	-48	0	-36	-47	2
		BA 28	14	5.52	-16	-20	-24	-16	-20	-19

Table 3

Clusters showing significantly increased BOLD response for observer memories. Reported statistics are based on a threshold of $p < 0.001$ (uncorrected) and a minimum cluster size of $k \geq 10$ contiguous voxels. Reported coordinates are for the cluster maxima, as defined by t -value; for clusters with multiple coordinates, local maxima are also reported. BA, Brodmann's area.

Hemi	Structure	Area	k	t	MNI coordinates			Talairach coordinates		
					X	Y	Z	X	Y	Z
Frontal										
Left	Medial frontal gyrus	BA 8	683	10.41	−16	32	44	−16	33	39
	Inferior frontal gyrus	BA 45		9.20	−52	20	12	−51	20	10
				9.12	−52	16	4	−51	16	3
Parietal–temporal										
Left	Inferior parietal lobule	BA 39	231	9.08	−48	−68	36	−48	−64	36
		BA 40		8.48	−44	−68	48	−44	−64	47
	Superior temporal gyrus	BA 39		7.81	−44	−60	28	−44	−57	29
Temporal–limbic										
Left	Middle temporal gyrus	BA 21	197	6.23	−60	−40	−8	−59	−39	−5
	Parahippocampal gyrus	BA 37		6.18	−36	−40	−8	−36	−39	−5
	Cingulate gyrus	BA 31		5.82	−20	−48	24	−20	−45	24
Cerebellum										
Right	Posterior lobe	Uvula	136	8.55	20	−76	−32	20	−75	−23
				8.39	20	−88	−36	20	−87	−26
				8.30	28	−80	−36	28	−79	−26
Parietal										
Right	Precuneus	BA 19	12	5.93	44	−76	40	44	−72	40
	Angular gyrus	BA 39		4.43	52	−72	28	51	−68	29
Sub-lobar										
Right	Thalamus	Pulvinar	30	5.56	12	−36	16	12	−34	16
	Caudate	Caudate tail		5.18	20	−44	16	20	−42	17
Limbic										
Right	Parahippocampal gyrus	BA 19	14	4.65	32	−44	−4	32	−43	−1

biographical events (Buckner, Andrews-Hanna, & Schacter, 2008; Buckner & Carroll, 2007; Cabeza et al., 2004; Conway et al., 1999; Wagner, Shannon, Kahn, & Buckner, 2005), a convergence of activation patterns supporting the normative validity of (1) our data and (2) our visual-search task as a baseline control for hemodynamic measurements.

The next step was to isolate those brain areas showing a significant difference in BOLD response between recall perspectives via direct comparisons between field and observer conditions. While no regions showed a greater response during observer relative to field retrieval, seven clusters showed a significantly greater block-related response for field relative to observer memories (Table 4). Of these clusters, only one – in the right posterior amygdala (pAMG) – had a positive BOLD response in the field condition (Fig. 4A), relative to the baseline control task. The remaining six clusters – including bilateral insula (INS), right posterior dorsal insula (pdINS), left secondary somatosensory area (SII), left motor and somatosensory strips (M1/S1), and left lateral occipital complex (LOC, not shown) – had BOLD responses that were significantly more negative for observer memories (Fig. 4B–F), relative to the baseline control task.

Paired t -tests on the mean block-related hemodynamic response (or β) within each of the clusters in Fig. 4 confirmed that the β in the field condition was significantly greater (or less negative) than the β in the observer condition ($ts(15) > 3.00$; $ps < 0.01$). Within each cluster, we then wanted to determine how the hemodynamic response was changing for each of the two memory conditions, relative to the baseline control task. Because the β s in a blocked fMRI design capture the relative changes between task and control blocks, if a given β is significantly greater than zero in a blocked design, then it indicates an increase in activity for task relative to control blocks. Likewise, if a given β is significantly less than zero, then it indicates a decrease in activity for task relative to control blocks. Accordingly, we used one-sample t -tests to isolate the direction of hemodynamic changes in each cluster for field and observer conditions, respectively, each relative to the baseline control task. These

t -tests confirmed that activity in the right pAMG increased above baseline blocks for field memories ($t(15) = 2.39$, $p < 0.05$) while the response for observer memories did not change significantly from baseline ($t(15) = 1.57$, $p > 0.10$). Likewise, responses in bilateral INS and right pdINS decreased below baseline for observer memories ($ts(15) > 4.10$, $ps < 0.01$) but not for field memories ($ts(15) < 1.80$, $ps > 0.10$); the responses in left SII, S1/M1 and left LOC dropped significantly below baseline for both field and observer memories ($ts(15) > 4.20$, $ps < 0.001$).

In sum, we identified three distinct sets of regions dissociating between field and observer memories, as measured relative to our baseline visual-search task: (1) bilateral INS and right pdINS selectively decreased in activity for observer memories, (2) left SII, M1/S1, and LOC decreased in activity during both retrieval conditions, but significantly less so for field relative to observer memories, and (3) the right pAMG selectively increased in activity for field memories.

Given that the number of internal and external statements made by participants during task recall were predictive of field and observer memories, respectively, the final step of our fMRI analysis was to control for memory content as a possible mediating factor in the regions identified above as having a differential response between recall perspectives. We first computed difference scores for each subject based on their task-recall narratives. For the internal statements predictive of field memories – namely, affective reactions, physical sensations, psychological states, and first-person accounts, per 100 words of recall narrative (Table 1C) – we subtracted the sum of such statements in the observer condition from the sum in the field condition. Conversely, for the external statements predictive of observer memories – physical actions, self-observations, and third-person accounts, again per 100 words of recall narrative (Table 1C) – we subtracted the total number of such statements in the field condition from the total number in the observer condition. We then correlated each of these difference scores with the anal-

Table 4 Clusters showing significantly increased BOLD response for field relative to observer memories. Reported statistics are based on a threshold of $p < 0.001$ (uncorrected) and a minimum cluster size of $k \geq 10$ contiguous voxels; because the amygdalae were an a priori region of interest and because reported activations in these structures are commonly in the 3–5 voxel range, we used a smaller extent threshold of $k \geq 3$ contiguous voxels specifically for these regions. Reported coordinates are for the cluster maxima, as defined by t -value; for clusters with multiple coordinates, local maxima are also reported. BA, Brodmann's area, βF , mean β for clusters associated with field memories, βO , mean β for clusters associated with observer memories.

Lobe	Location	BA	k	t	βF	βO	MNI coordinates			Talairach coordinates		
							X	Y	Z	X	Y	Z
Occipital	Middle occipital gyrus	18	31	8.88	-0.70	-0.89	-24	-96	16	-24	-92	19
				4.71			-40	-92	8	-40	-89	12
Frontal–parietal	Inferior occipital gyrus	4	92	4.45	-0.23	-0.41	-48	-80	-4	-48	-78	1
				6.23			-36	-28	60	-36	-24	56
				5.94			-44	-16	60	-44	-13	56
Frontal–sub-lobar	Postcentral gyrus	3	38	5.84	-0.05	-0.21	-48	-16	52	-48	-13	49
				5.33			56	-4	8	55	-4	8
				5.14			44	-8	8	44	-7	8
Parietal	Insula	40	15	4.89	-0.13	-0.30	40	0	8	40	0	7
				5.06			-56	-28	24	-55	-26	23
Sub-lobar	Inferior parietal lobule	13	21	4.99	-0.06	-0.20	-40	-4	0	-40	-4	0
				4.86			-36	0	12	-36	11	11
Sub-lobar–temporal	Insula	13	15	4.13	-0.04	-0.18	-40	-16	12	-40	-15	12
				4.64			48	-32	20	48	-30	20
Sub-lobar	Superior temporal gyrus	41	4	4.19	0.12	-0.06	44	-36	4	44	-35	5
				4.36			28	-12	-16	28	-12	-13

ogous difference scores in the hemodynamic response (or β) between recall perspectives: field β minus observer β for the internal variable, and observer β minus field β for the external variable.

Because our goal in this analysis was to examine whether there was any overlap between regions showing a sensitivity to recall perspective versus memory content per se, we used a relatively liberal statistical threshold ($p < 0.01$, uncorrected) for all correlations in order to minimize Type II error rates (i.e., the more conservative statistical approach for this analysis was to use a more liberal statistical threshold). For internal memory content, six voxel clusters showed positive correlations with hemodynamic activity that were significant at a threshold of $p < 0.01$, uncorrected (Fig. 5 and Table 5). These clusters corresponded to the right orbitofrontal cortex (OFC, Fig. 5A), left entorhinal cortex (Fig. 5B), right lingual gyrus (Fig. 5C), right middle temporal gyrus (MTG, Fig. 5D), right superior temporal sulcus (STS, Fig. 5E) and left lateral occipital complex (LOC, Fig. 5F). For external memory content, no voxels clusters showed significant positive correlations with hemodynamic activity. These analyses thus revealed little, if any, overlap between regions showing a sensitivity to recall perspective (Fig. 4) versus the subjective content of retrieved memories (Fig. 5).

To confirm this observation, we also computed field minus observer difference scores for subjective ratings of emotionality, and correlated these values with the analogous hemodynamic difference scores (field β minus observer β). Four voxel clusters showed significant positive correlations (Fig. 6 and Table 6). These clusters included the left inferior frontal gyrus (IFG, Fig. 6A), left middle frontal gyrus (MFG, Fig. 6B), left precentral gyrus (pre-CENTG, Fig. 6C), and right superior insula (sINS, Fig. 6D). Once again, there was no clear overlap with regions sensitive to retrieval perspective itself.

4. Discussion

Evidence from several behavioral sources suggests that memories relived from a field or first-person perspective have an increased level of subjective emotionality, relative to memories retrieved from an observer or third-person perspective (e.g., McIsaac & Eich, 2002; Nigro & Neisser, 1983; Robinson & Swanson, 1993). This study sought to identify the neural systems mediating this effect. More to the point, a number of different brain regions have been reliably implicated in autobiographical memory retrieval unconstrained for visual perspective, including prefrontal and medial temporal cortices, inferior parietal lobule, and pre-cuneus (e.g., Cabeza et al., 2004; Conway et al., 1999; Wagner et al., 2005; for reviews, see Cabeza & St. Jacques, 2007; Svoboda, McKinnon, & Levine, 2006). We confirmed that this basic network of cortical areas is engaged regardless of retrieval perspective and the subsequent differences that emerge in the subjective emotionality and narrative content of the actual memories retrieved.

More importantly, our results showed that retrieval perspective influenced hemodynamic activity in an additional network of brain regions: the bilateral insula, left somatosensory areas, and the right posterior dorsal amygdala (Fig. 7). Further, these areas dissociated in their relative response profiles across retrieval conditions: the insula regions selectively decreased in activity during observer memories, the somatosensory regions showed greater decreases in activity during observer relative to field memories, and the right amygdala selectively increased in activity for field memories. Notably, these responses could not be ascribed to individual variability either in memory content per se (Fig. 5) or in subjective ratings of emotionality (Fig. 6). Instead, the responses were specific to the given mode of retrieval itself, and we thus propose that these regions represent key subcompo-

Field > Observer

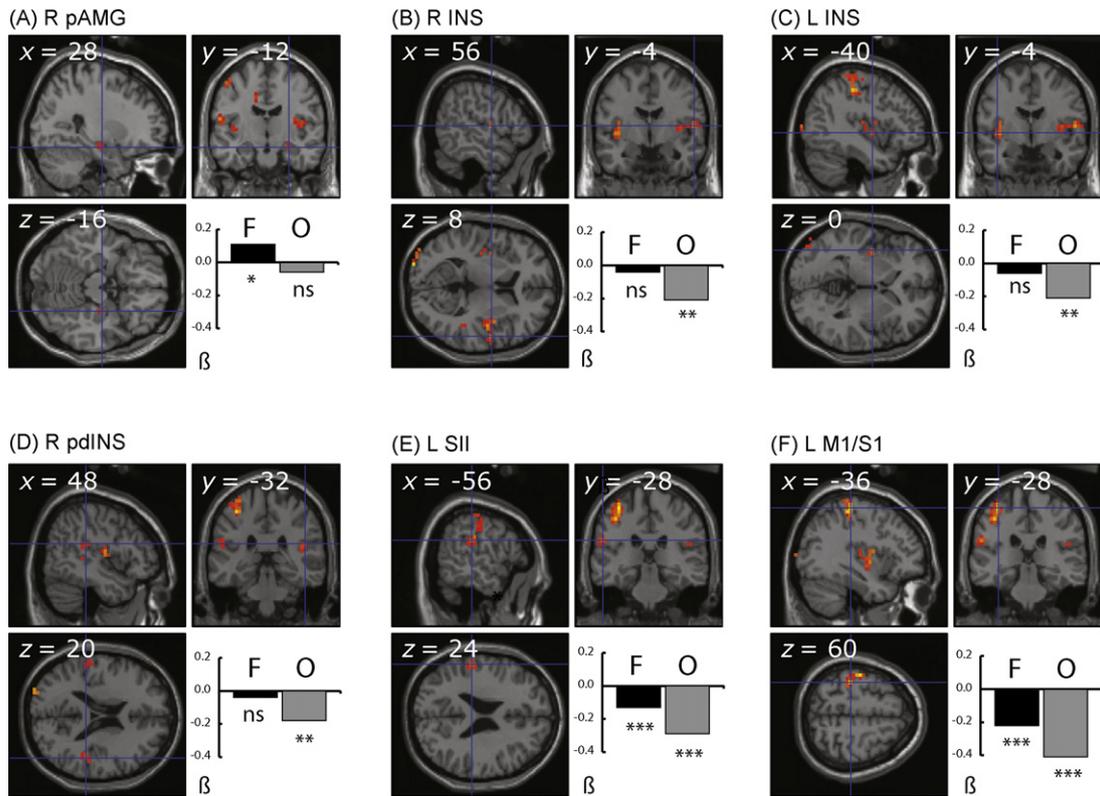


Fig. 4. Field versus observer differences. We identified three sets of regions dissociating field and observer memories. First, the right posterior amygdala (pAMG, A) showed a relative increase in hemodynamic activity for field memories. Second, the right and left insulae (INS, B and C) and the right posterior dorsal insula (pdINS, D) showed a relative decrease in hemodynamic activity for observer memories. Finally, in left secondary somatosensory area (SII, E), left motor and somatosensory strips (M1/S1, F), and left lateral occipital complex (not shown) activity decreased less for field relative to observer memories. Plotted is the mean hemodynamic response (β) for each cluster as a function of retrieval condition (black = field/F, gray = observer/O), where the difference was significant at * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$. Clusters are shown on the MNI anatomical template provided with SPM2. All data were based on a threshold of $p < 0.001$ (uncorrected). L, left; R, right.

Table 5

Clusters showing significant positive correlation between internal memory content and BOLD response, both based on difference scores (field minus observer). Reported statistics are based on a threshold of $p < 0.01$ (uncorrected) and a minimum cluster size of $k \geq 10$ contiguous voxels. Reported coordinates are for the cluster maxima, as defined by t -value. BA, Brodmann's area, r , mean correlation across all voxels in cluster.

Lobe	Hemi	Location	BA	k	t	r	MNI coordinates			Talairach coordinates		
							X	Y	Z	X	Y	Z
Frontal	R	Anterior cingulate gyrus	32	20	4.56	0.731	16	40	-8	16	38	-9
Temporal	L	Parahippocampal gyrus	35	19	3.98	0.726	-28	-12	-28	-28	-13	-23
Temporal	R	Superior temporal gyrus	22	10	3.75	0.706	68	-20	4	67	-19	5
Temporal	R	Middle temporal gyrus	39	13	3.67	0.722	48	-56	4	48	-54	6
Occipital	R	Lingual gyrus	19	12	3.43	0.680	28	-72	-4	28	-70	0
Occipital	L	Middle occipital gyrus	19	13	3.38	0.722	-44	-84	4	-44	-81	8

nents of the autobiographical memory retrieval network that vary with the visual perspective taken during retrieval. Several discussion points follow that highlight the broader implications of our findings.

4.1. Autobiographical memory and emotion

It has recently been suggested that the subjective emotionality of autobiographical memories, in terms of both arousal and valence,

Table 6

Clusters showing significant positive correlation between subjective rating of emotionality and BOLD response difference scores (field minus observer). Reported statistics are based on a threshold of $p < 0.01$ (uncorrected) and a minimum cluster size of $k \geq 10$ contiguous voxels. Reported coordinates are for the cluster maxima, as defined by t -value. BA, Brodmann's area, r , mean correlation across all voxels in cluster.

Lobe	Hemi	Location	BA	k	t	r	MNI coordinates			Talairach coordinates		
							X	Y	Z	X	Y	Z
Frontal	L	Middle frontal gyrus	10	27	5.76	0.750	-36	48	0	-36	47	-2
Frontal	R	Precentral gyrus	13	29	5.53	0.723	32	-4	20	32	-3	19
Frontal	L	Precentral gyrus	44	15	4.17	0.678	-52	0	12	-51	1	11
Frontal	L	Inferior frontal gyrus	47	17	3.42	0.750	-36	24	-16	-36	23	-15

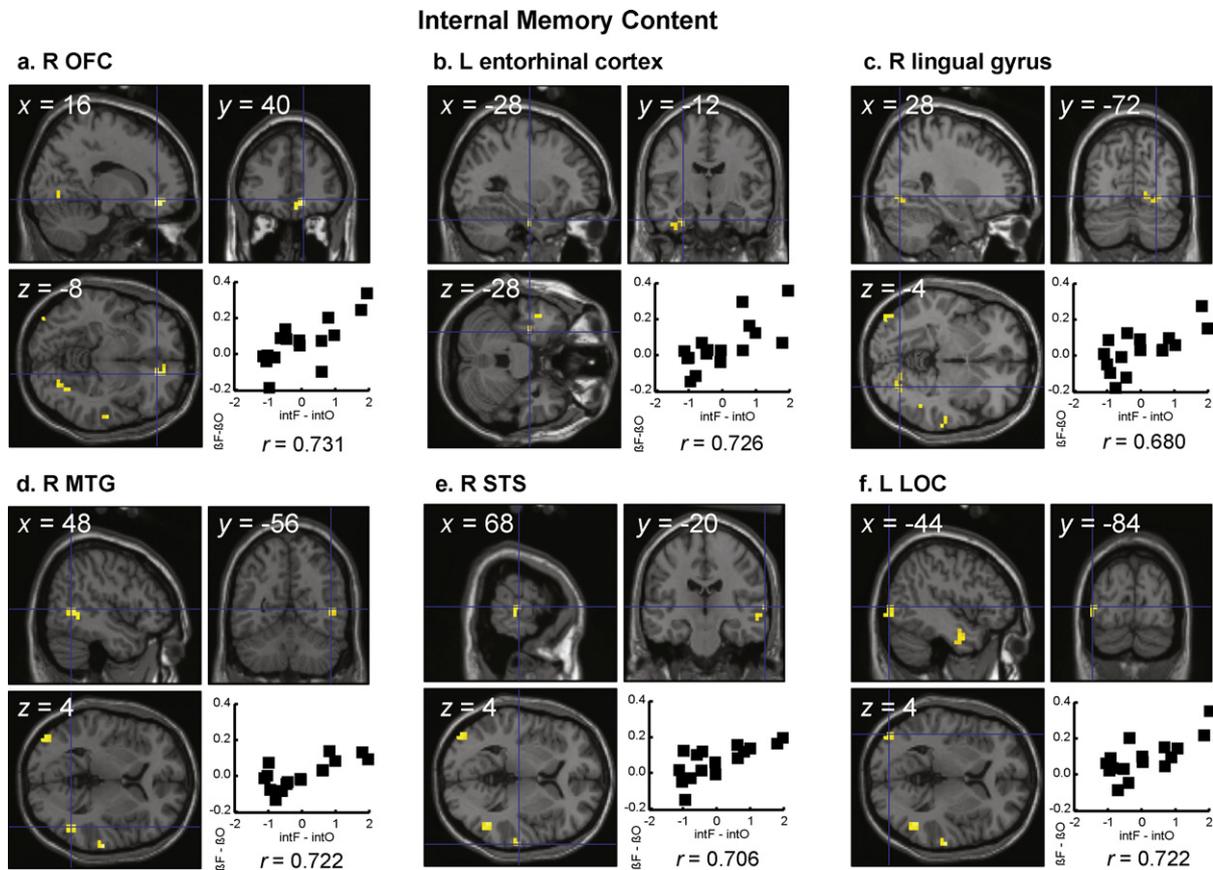


Fig. 5. Brain areas correlating with internal memory content. The six cortical regions showing significant positive correlations between the internal memory content variable and hemodynamic activity (or β): right orbitofrontal cortex (OFC, A), left entorhinal cortex (B), right lingual gyrus (C), right middle temporal gyrus, D), right STS (E), and left lateral occipital complex (LOC, F). Regression in SPM2 was based on a threshold of $p < 0.01$, in order to minimize Type II error rates; r = correlation coefficient for each cluster; clusters are shown on the MNI anatomical template provided with SPM2.

is associated with the amygdala (Cabeza & St. Jacques, 2007). For example, not only does the amygdala play a role in the encoding and consolidation of emotional memories (e.g., McGaugh, 2004; Phelps, 2004), but it has also been implicated in the retrieval of such memories as well (e.g., Fink et al., 1996; Smith et al., 2004). While our finding of increased activity in the right amygdala specifically during field memories – memories which showed greater subjective emotionality relative to observer memories – is certainly consistent with this proposal, our results suggest that other brain regions may also be involved in mediating the emotionality of autobiographical memories.

In particular, the insula and somatosensory cortices S1 and SII have been implicated as the key neural systems underlying interoception-based awareness of one's current emotional state (Critchley et al., 2004; Damasio et al., 2000; Pollatos et al., 2006). That we found decreased activity in the insula during observer memories, and significantly greater decreases in activity in S1 for observer relative to field memories supports the hypothesis that the emotionality of autobiographical memories – and field autobiographical memories, more specifically – depends on the engagement of interoceptive-based functions in these regions, in addition to any involvement of the amygdala. Given the amygdala's role in the affective appraisal of on-going perceptual events (LaBar, 2007), the idea our data converge on is that memory emotionality may include appraisal of both memoranda per se (as mediated by the amygdala) and one's visceral/emotional state (as mediated by the insula and somatosensory regions).

With that said, our results advance our basic understanding of emotionality in memory retrieval in two additional ways. First, they suggest that emotionality in memory retrieval is not limited to con-

ditions involving affectively extreme events. The tasks carried out by participants in our study, while arguably memorable, nevertheless represent the banalities of everyday life such as walking, cooking, and playing games. Second, our findings demonstrate that activation of emotion-related brain regions during autobiographical memory retrieval does not depend on comparing between distinct memories with different valences. Rather, the fact that our study held memory events constant implies that the mode of retrieval itself – which is what we varied rather than memory valence per se – can be sufficient to modulate emotional responses at both the cognitive and neural level.

Taken together, these observations converge on the idea that adopting a first-person perspective during autobiographical retrieval results in an increased level of affective monitoring, regardless of the overall valence of the memory content being retrieved. If tenable, this possibility also helps explain why some studies have not reported amygdala activations during autobiographical retrieval (Keedwell, Andrew, Williams, Brammer, & Phillips, 2005; Piefke, Weiss, Zilles, Markowitsch, & Fink, 2003). Specifically, one would predict that under experimental conditions that do not control for retrieval perspective, the likelihood of finding amygdala activation will decrease with increasing proportions of third-person retrieval mode, all else being equal. That said, an important caveat is that our hypothesis does not preclude an effect of valence per se on amygdala activation during retrieval. Indeed, given the variety of amygdala activations that have been reported – left lateralized (Daselaar et al., 2008), right lateralized (Dolcos et al., 2005), and bilateral (Greenberg et al., 2005) – it seems almost certain that the amygdala is sensitive to multiple retrieval-related factors.

Subjective Emotionality Ratings

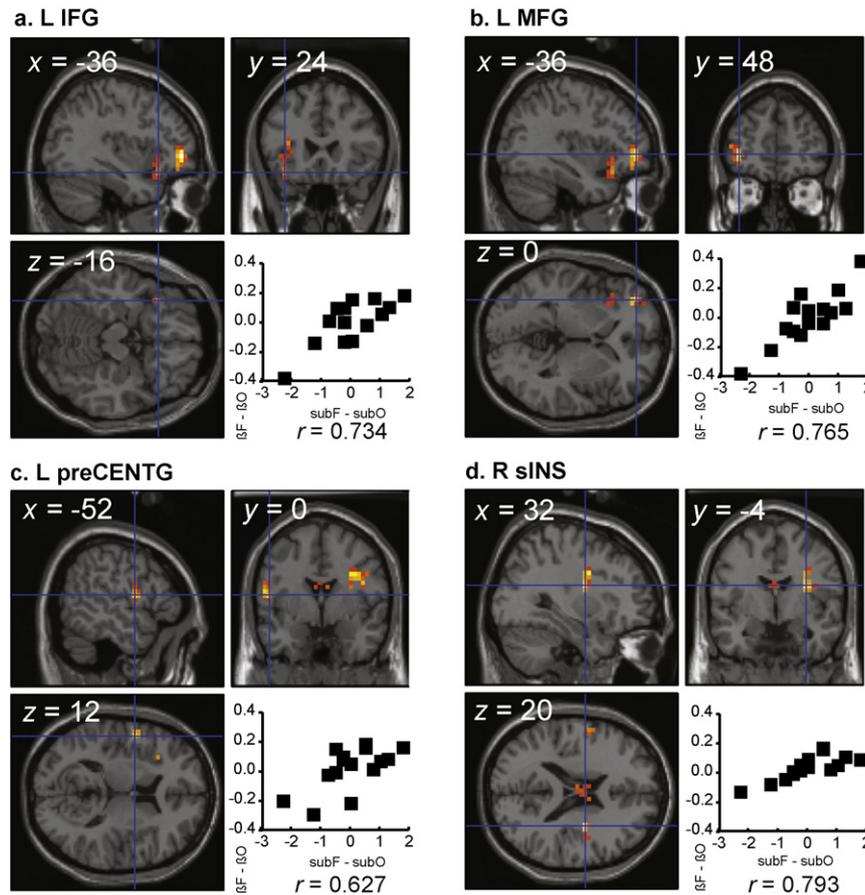


Fig. 6. Brain areas correlating with subjective emotionality ratings. The four cortical regions showing significant positive correlations between the subjective rating of memory emotionality and hemodynamic activity (β): the left inferior frontal gyrus (IFG, A), left middle frontal gyrus (MFG, B), left precentral gyrus (preCENTG, C), and right superior insula (sINS, D). Regression in SPM2 was based on a threshold of $p < 0.01$, in order to minimize Type II error rates; r = correlation coefficient for each cluster; clusters are shown on the MNI anatomical template provided with SPM2.

A final point to make regarding the amygdala activation we report concerns its relatively posterior location. In particular, it might be argued that the cluster actually falls into the anterior portion of the hippocampus rather than the posterior portion of the amygdala. However, at least two lines of evidence are consistent with our labeling of “amygdala.” First, while amygdala activations reported in the literature are typically more anterior, others have reported amygdalar responses at posterior locations equivalent to ours here (e.g., Gottfried, O’Doherty, & Dolan, 2002). Second, high-resolution volumetric imaging of the amygdala/hippocampus region indicates that the posterior portion of the amygdala overlaps with the anterior tip of the hippocampus such that, in coronal sections across these overlapping regions, the posterior end of the amygdala becomes increasingly dorsomedial to the hippocampus (Pruessner et al., 2000)—a location consistent with the orientation of our cluster maxima in the amygdalar/hippocampal region. Nevertheless, we stress that our main conclusion – field memories engage emotion-related brain regions more so than observer memories – stands regardless of the extent to which the amygdala may be involved.

4.2. Memory and perspective taking

A key aspect of our fMRI results is that we discerned a functional dissociation between insular and somatosensory regions, the former showing selective decreases in activity for observer memories but the latter showing significantly greater decreases in activity for

observer relative to field memories. While we ascribe the effect of retrieval condition on activity in these regions to the greater emotionality of field versus observer memories as discussed above, there also appears to be an additional factor differentially affecting insular versus somatosensory regions as well.

To the point, recent evidence has shown that observing or imitating simple physical actions from a first- rather than a third-person perspective results in greater activation of sensory-motor systems in cortex (Jackson, Meltzoff, & Decety, 2006). While our study focused on retrospective autobiographical memory, rather than real-time visual perception, the critical manipulation nevertheless concerned visual perspective taking. Thus it is interesting to note that while first-person retrieval certainly resulted in decreased activity in left S1 and SII (and M1 as well), this decrease was significantly less than the decreases in these regions during third-person retrieval. This suggests that while there may be overall decreases in activity within sensory-motor regions during memory retrieval, field memories seem to retain a greater degree of somatosensory involvement than do observer memories, their disembodied analogs.

4.3. Memory and the self

In conclusion, our results indicate that taking a third-person perspective during autobiographical memory retrieval appears to significantly decrease activity in regions of cortex associated with interoceptive awareness. To be clear, while we cannot unambigu-

Retrieval Systems

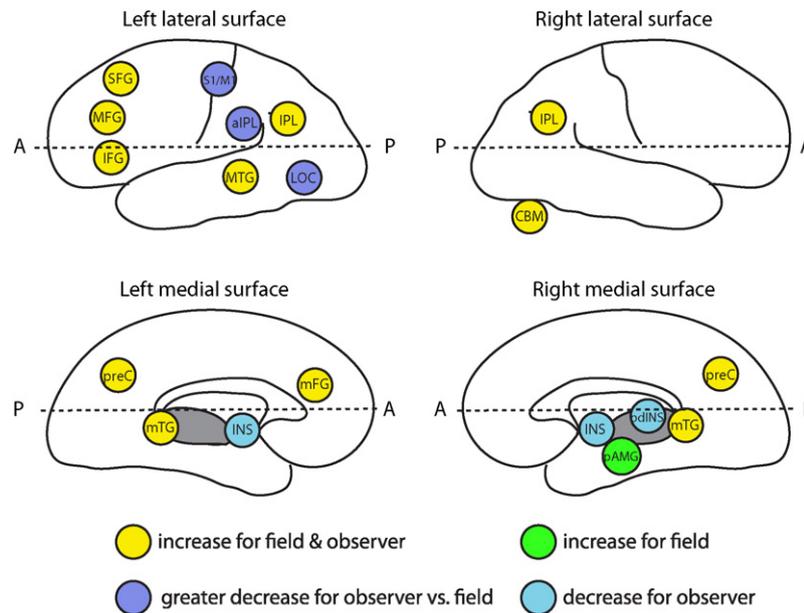


Fig. 7. A schematic summary of the brain networks associated with the retrieval of field and observer memories. Areas in yellow are common to memory retrieval regardless of the perspective taken. The areas in blue decreased in activity specifically during observer memories, the areas in purple showed greater decreases in activity for observer relative to field memories, and the area in green showed an increase in activity specifically during field memories. SFG, superior frontal gyrus; MFG, middle frontal gyrus; IFG, inferior frontal gyrus; aIPL, anterior inferior parietal lobule; IPL, inferior parietal lobule; MTG, middle temporal gyrus; LOC, lateral occipital cortex; CBM, cerebellum; preC, precuneus; mTG, medial temporal gyrus; INS, insula; mFG, medial frontal gyrus; pdINS, posterior dorsal insula; pAMG, posterior amygdala. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

ously establish causality as to whether the retrieval mode itself directly inhibited these regions, or whether reduced activity in this system followed from the content of the retrieved memories, two key inferences may nevertheless be drawn regarding memory and self-representation.

First, there has been growing interest in understanding the brain's default mode of operation, in terms of what functions and networks are "on" as a baseline state (Buckner et al., 2008; Schacter et al., 2007). In this regard, the greater relative decreases we found in insular and left somatosensory regions during the recall of observer memories was ultimately measured relative to our visual-search task used as a cognitively active control. In practical terms, this means that these regions may collectively represent a network that is "on" by default and that specifically "turns off" when adopting a third-person perspective during memory retrieval. Moreover, this network appears to be dissociable, on both anatomical and functional grounds, from the so-called "default network" – including anterior and posterior cingulate cortex – that has been linked to passive cognitive states (e.g., Mason et al., 2007; Raichle et al., 2001), where the mind is relatively disengaged from the external environment (Smallwood, Beach, Schooler, & Handy, 2008). The implication, then, is that the brain independently monitors the internal versus external milieu, with each monitoring system having its own neural network and default state.

Second, the idea of the self as a conceptual reference point for evaluative processing has recently emerged as an important form of subjective self-representation in the human brain that has been linked to ventromedial frontal and prefrontal cortices (Kelley et al., 2002). In considering the role that self-referencing plays in cognitive processing, our results suggest that subjective self-referencing also includes a sense of physical or "somatic" self – mediated in insular and somato-motor cortices – that is distinct from what we might call the "conceptual" self. Of interest is not just the distinction itself, but what our data underscore in regards to the dynamic nature of the self-representations them-

selves: in both cases, the representation of self is strongly reactive to subjective manipulation. Whereas the intensity of self-referential processing directly modulates activity in the "conceptual" self network (Turk, Heatherton, Macrae, Kelley, & Gazzaniga, 2003), here we show how shifting one's spatial perspective during memory retrieval directly modulates activity in the "somatic" self network. As such, the present results add new meaning to the psychological concept of self and aid neuroscientific understanding of its central role in autobiographical memory.

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