Functional Neuroimaging of Sex Differences in Autobiographical Memory Recall

Kymberly D. Young,^{1,*} Patrick S.F. Bellgowan,^{1,2} Jerzy Bodurka,¹ and Wayne C. Drevets^{1,3}

¹Laureate Institute for Brain Research, Tulsa, Oklahoma

²Faculty of Community Medicine, The University of Tulsa, Tulsa, Oklahoma

³Department of Psychiatry, The University of Oklahoma College of Medicine, Tulsa, Oklahoma

Abstract: Autobiographical memory (AM) is episodic memory for personally experienced events. The brain areas underlying AM retrieval are known to include several prefrontal cortical and medial temporal lobe regions. Sex differences in AM recall have been reported in several behavioral studies, but the functional anatomical correlates underlying such differences remain unclear. This study used fMRI to compare the neural correlates of AM recall between healthy male and female participants ($n = 20$ per group). AM recall in response to positive, negative, and neutral cue words was compared to a semantic memory task involving the generation of examples from a category using emotionally valenced cues. Behaviorally, females recalled more negative and fewer positive AMs compared with males, while ratings of arousal, vividness, and memory age did not differ significantly between sexes. Males and females also did not differ significantly in their performance on control tasks. Neurophysiologically, females showed increased hemodynamic activity compared to males in the dorsolateral prefrontal cortex (DLPFC), dorsal anterior insula, and precuneus while recalling specific AMs (all valences combined); increased activity in the DLPFC, transverse temporal gyrus, and precuneus while recalling positive AMs; and increased activity in the anterior cingulate cortex, precuneus, amygdala, and temporopolar cortex when recalling negative AMs. When comparing positive to negative AMs directly, males and females differed in their BOLD responses in the hippocampus and DLPFC. We propose that the differential hemodynamic changes may reflect sex-specific cognitive strategies during recall of AMs irrespective of the phenomenological properties of those memories. *Hum Brain Mapp* 34:3320–3332, 2013. © 2012 Wiley Periodicals, Inc.

Key words: autobiographical memory; episodic memory; sex differences; fMRI; cognition; emotion

INTRODUCTION

Autobiographical memory (AM) is episodic memory of personally experienced events that occurred at a particular time and place [Tulving, 2002]. The neurobiological substrates that support AM retrieval have been researched extensively in healthy humans using functional neuroimaging. These studies have shown that AM retrieval involves the hippocampus (e.g., Addis et al., 2004; Fink et al., 1996), anterior cingulate cortex (ACC), and posterior cingulate cortex [e.g., Addis et al., 2004; Denkova et al., 2006; Gardini et al., 2006; Ryan et al., 2001], temporoparietal cortex [Addis et al., 2004; Cabeza et al., 2004; Maguire and Frith, 2003], dorsolateral prefrontal cortex (DLPFC;

Contract grant sponsor: Laureate Institute for Brain Research and the William K. Warren Foundation.

*Correspondence to: Kymberly D. Young, Laureate Institute for Brain Research, 6655 South Yale Avenue, Tulsa, OK 74136. E-mail: kyoung@laureateinstitute.org

Received for publication 12 March 2012; Revised 4 May 2012; Accepted 16 May 2012

DOI: 10.1002/hbm.22144

Published online 17 July 2012 in Wiley Online Library (wileyonlinelibrary.com).

Cabeza et al., 2004; Conway et al., 1999; Levine et al., 2004), and ventrolateral prefrontal cortex [VLPFC; Cabeza et al., 2004; Maguire et al., 2001; Piefke et al., 2003].

Behaviorally, sex differences in AM recall have been reported in some studies. Studies have found that females are significantly faster to recall AMs than males, and recall AMs that are more detailed and emotionally intense than those recalled by males [Andreano and Cahill, 2009; Davis, 1999; Seidlitz and Diener, 1998]. Other studies have failed to find sex differences in AM recall [Piefke et al., 2005; Rubin et al., 1999; St Jacques et al., 2010]. In the studies that obtained positive results, two hypotheses have been offered to explain reported sex differences in AM recall. The “affect intensity hypothesis” proposes that sex differences arise from increased emotional processing or elaborative rehearsal in females which results in deeper encoding [Fujita et al., 1991]. The “cognitive styles hypothesis” proposes that the use of different cognitive strategies during AM encoding and recall results in observed differences such that men use spatial contextual strategies while females use verbal recall strategies [Seidlitz and Diener, 1998].

The functional anatomical basis of potential sex differences in AM recall is not well understood. To date, two studies have used neuroimaging to examine sex differences in AM recall, and the researchers interpreted their imaging results as supporting the cognitive styles hypothesis of sex differences, reportedly indicating that males used a more spatially oriented approach to AM recall. Piefke et al. [2005] found that males showed increased activity in the left parahippocampal gyrus, while females had increased activity in the right insula and DLPFC while recalling AMs collected during a prescan interview compared to an attentional task involving detection of a checkerboard pattern. These functional differences were observed in the absence of any observed behavioral differences, and so their functional significance remained unclear. St Jacques et al. [2010] found males had increased activity in the left inferior frontal gyrus, the hippocampus, and the retrosplenial and occipital cortices while retrieving AMs elicited using video images recorded using a SenseCam that had been attached to the participants during the week prior to scanning compared to Fourier-transformations of the same images. These researchers also found these physiological differences in the absence of observed behavioral differences, however, obscuring their functional significance. Moreover, when AM retrieval was cued instead via verbal descriptions provided by participants of the previous weeks’ events compared to letter string presentation, no sex difference in regional hemodynamic activity was observed.

Interestingly, both studies used a recognition paradigm of AM recall, where memories used in the scanner had been collected previously, either via a prescan interview or by keeping a written journal of events, or pictures taken from the previous week. It is conceivable that recalling the memories prior to fMRI scanning during a pre-specified,

experimental time period [Piefke et al., 2005] or creating cues based on events intentionally recorded by participants [St Jacques et al., 2010] might change the properties of the memories themselves [Conway et al., 2002; Ryan et al., 2001]. Therefore, these studies may not precisely assess AM recall. The goal of this study was to further investigate differences in the hemodynamic response between healthy males and females as they recalled AMs. Participants were presented with cue words and instructed to generate a specific AM before rating their memory on several dimensions. We predicted that similar to previous studies, males would show increased activity in medial temporal regions, while females would show increased activity in PFC areas.

METHOD

Participants

Forty psychiatrically and medically healthy, right-handed participants between the ages of 18 and 55 years (20 males) participated in this study. Volunteers were recruited from the community via advertisements and evaluated at the Laureate Institute for Brain Research. Volunteers underwent medical and psychiatric screening evaluations that included structured diagnostic assessments for personal or family history of psychiatric disorders using the Structural Clinical Interview for DSM-IV disorders [SCID; First et al., 1995], and the Family Interview for Genetic Studies [FIGS; Maxwell, 1992]. Exclusion criteria included major medical or neurological disorders and exposure to any medication likely to influence CNS function within the three weeks prior to entry. Volunteers with a personal or family history of a major psychiatric disorder, and individuals who met DSM-IV criteria for alcohol and/or substance abuse within the previous 1 year, or for a lifetime history of substance dependence (excepting nicotine) were excluded. After receiving a complete explanation of the study procedures, all participants provided written informed consent as approved by the Western IRB. Participants received financial compensation for their participation. Research was performed in compliance with the Code of Ethics of the World Medical Association and the standards established by the Western IRB.

Intelligence testing was performed using the two-subtest version of the Wechsler Abbreviated Scale of Intelligence [Wechsler, 1999]. Anxiety and depressive symptoms were rated on the day of scanning using the State-Trait Anxiety Inventory [Spielberger, 1983] and the 21-item Hamilton Rating Scale for Depression [HRSD; Hamilton, 1960].

fMRI Data Acquisition

The fMRI scans were obtained using a 3T GE 750 MR scanner, with an eight-channel receiver coil array (GE Healthcare, USA). Gradient-recalled, echoplanar imaging

(EPI) with sensitivity (SENSE) was used for fMRI with the following parameters: $40 \times 3 \text{ mm}^2$ slices acquired axially, repetition time (TR) = 2,000 ms, echo time (TE) = 25 ms, SENSE acceleration = 2, flip angle = 90° , matrix = 96×96 , field of view (FOV) = 24 cm, voxel volume = $2.5 \times 2.5 \times 3 \text{ mm}^3$. A total of 211 EPI images were acquired in each of ten 7-min runs during the fMRI task. The first four images of each run were discarded to allow for steady-state tissue magnetization. High-resolution T1 weighted anatomical MRI scans ($120 \times 1.2 \text{ mm}$ slices acquired axially, TR = 5 ms, TE = 1.93 ms, flip angle = 8° , matrix = 256×256 , field of view (FOV) = 24 cm, in-plane resolution = 0.94 mm^2) also were acquired for co-registration with the EPI series.

fMRI Autobiographical Memory Task

Prior to scanning participants received instruction about performing the behavioral task, and were presented with three practice cue words. Additionally, participants were instructed as to the different types of AMs they might retrieve (according to conventional definitions used in the AM literature [e.g., Anderson et al., 2009; Williams and Scott, 1988; Williams et al., 2007]), and were informed that their goal was to recall specific AMs. A specific memory was defined as a memory for an event that occurred at an identified place and did not last longer than one day. That is, a memory was specific if the participant was able to specify an epoch when the episode occurred (e.g., “attending Jane’s party last Friday”). A categorical memory was defined as referring to a category of events containing a number of specific episodes without reference to one specific event (e.g., “all the times I’ve failed an exam”). An extended memory was defined as a memory that referred to an extended period of time without reference to a specific event within the time frame (e.g., a week long vacation; a semester at school). A semantic memory was defined as a statement of fact without an associated event (e.g., “I have never been to a dance”). Participants were provided with these definitions verbally prior to entering the scanner gantry, and immediately prior to each fMRI run.

A computerized version of the AM task [Williams and Broadbent, 1986] was developed for use during fMRI. Participants were presented 60 words (20 positive, 20 negative, 20 neutral; Bradley and Lang, 1999) using E-Prime software (Psychology Software Tools, USA). During fMRI, participants were presented with a cue word for 12 s and instructed to recall a past experience. Following the cue word, participants rated the retrieved memory on the specificity (specific, categorical, extended, semantic, repeat, or no memory) and the valence (negative, somewhat negative, neutral, somewhat positive, positive, no memory). Participants had 10 s to assign each rating by scrolling to the relevant option and selecting it using a scroll wheel (Current Designs, USA).

The AM recall condition was compared to a semantic recall condition (example generation) to control for abstract/general knowledge retrieval [Conway, 1992]. For this comparison task, participants were presented with a category cue word for 12 s and instructed to think of at least seven examples from that category (e.g., tools). Ten positive, 10 negative, and 10 neutral categories (selected from the same word pool as the memory cue words and matched to memory cue words for frequency of use in the English language, valence, and arousal) were presented. Following the category cue word, participants rated the ease with which they were able to generate examples (very easy, easy, somewhat easy, somewhat difficult, difficult, very difficult) and the number of examples they were able to generate (0, 1-2, 3-4, 5-6, 7, 8 or more). Participants had 10 s to select each rating.

Following the presentation of each memory/category cue word and each set of ratings, participants engaged in a riser detection task as a control for visual input/attention. All category and cue words were scrambled into lowercase nonword letter strings and participants were instructed to count the number of risers in the string. A riser was defined a letter with a part rising above the tops of the other letters (e.g., “gtulmnh” has the risers t, l, and h). The presentation of each letter string was jittered with an average presentation time of 6 s. For a randomly selected one-half of these strings, a 2-s period followed where participants selected whether the number of risers in the previous string was even or odd.

The order of memory and category cue word presentations was pseudo-randomized with restrictions on order presentation to prevent sequential presentations of a particular valence. Within each of ten 7-min runs, participants were presented with six memory cue words, three category cue words, and 18 riser letter strings in the order: cue word—riser (1/2 followed by odd/even question)—ratings—riser (1/2 followed by odd/even question). Two computers time-linked to the image acquisition of the MRI scanner controlled stimulus presentation and behavioral response collection. Participants observe the stimuli using a mirror system attached to the head coil.

Following the scan, the experimenter presented participants with all of the AM cue words again in the same order as during the scan. Participants were asked to describe the memory in detail to allow the experimenter to corroborate participants’ ratings of specificity during the scan. In addition to the definitions provided above, the experimenter also included a “can’t recall” category. A memory was categorized as can’t recall if either the participant was unable to recall the memory retrieved during fMRI or the memory provided did not match the specificity rating given by the participant (indicating they had not reported the same memory as that retrieved during the scan). Participants also rated each memory on three additional properties: Arousal (five point scale ranging from very low to very high), vividness (five point scale ranging from “not at all vivid” to “perfectly clear

and vivid") and age when memory occurred (childhood, adolescence, adulthood after age 18 but greater than 1 year prior to scan, adulthood between 6 months and 1 year prior to scan, adulthood within 6 months prior to scan). With respect to arousal and vividness ratings, participants were instructed to make these ratings based on how the memory was making them feel "at the time of recall," rather than how they felt at the time the remembered event occurred.

Assessment of Behavioral Performance During fMRI

Behavioral data were analyzed using SYSTAT 13 (Systat Software Inc., USA). Potential group differences in age, IQ, anxiety ratings, performance on the riser detection and example generation control tasks, and the percent of memories recalled at each specificity level (specific, categorical, extended, semantic, repeat, no memory, and can't recall post-scan) were assessed using unpaired *t*-tests. Although no group difference was expected on these characteristics, these assessments explored whether a nonspecific group difference may have confounded any difference identified in the AM retrieval condition; thus the associated *P*-values were not corrected for multiple testing.

The a priori hypothesis testing focused on the properties of the specific memories, as too few exemplars of the other types of AMs were retrieved to allow for sufficient power to detect behavioral or neurophysiological differences. To increase power, the following variables were collapsed: low and very low arousal were considered together to generate a low arousal variable, high and very high arousal to produce a high arousal variable, low, and very low vividness to produce a low vividness variable, high, and very high vividness to create a high vividness variable, somewhat positive and positive to create a positive variable, and somewhat negative and negative to create a negative variable. Repeated measures ANOVAs were performed for the between subjects variable Sex, the repeated measures of Valence (positive, negative, neutral) and either Arousal (low, medium, high), Vividness (low, medium, high), or Age (childhood, adolescence, after 18 but longer than 1 year prior to scan, between 6 months and one year prior to scan, and less than 6 months before scan) for the dependent variable Percent of Memories recalled. Follow up paired samples *t* tests were conducted to contrast the percent of memories recalled for significant results within the repeated measures ANOVAs. The threshold criterion for significance was set at $P < 0.05$, corrected for multiple comparisons (Bonferroni).

fMRI Processing and Analysis

Image preprocessing and analysis were performed using AFNI (<http://afni.nimh.nih.gov/afni>). Image preprocess-

ing consisted of slice acquisition time correction, within-subject realignment, coregistration between the anatomical and functional images, spatial normalization to the stereotaxic array of Talairach and Tournoux [1988], and smoothing using a 4 mm full-width at half-maximum Gaussian kernel. This smoothing kernel was selected because we were particularly interested in small medial temporal lobe structures such as the amygdala, hippocampus, and parahippocampus, and previous studies have shown that applying a relatively small smoothing kernel (between 3 and 6 mm) during image processing optimized the sensitivity for detecting BOLD signal changes in such structures [Skudlarski et al., 1999]. Using 3dDeconvolve for each participant, the hemodynamic response to each event type was modeled as a boxcar function convolved with a synthetic hemodynamic response function. Regressors modeling the task and motion parameters were used in the model. The main effects-of-interest were the cue word presentations that prompted specific memory recall and example generation. The entire 12-s window following cue presentation was included. In addition to regressors modeling the main effects, each design matrix included regressors modeling rating selection, cue presentation where the retrieved memory was not recalled, cue presentation where other types of memories were recalled (extended, semantic, categorical), and even/odd riser question presentations. The nonword letter strings used as stimuli for the riser detection task were modeled as the baseline. Using 3dREMLfit (restricted maximum likelihood of the regression parameters and variance), the generalized least squares time series fit was generated for each participant. The output from this program was used for group comparisons.

At the group level, 3dMEMA (mixed-effects meta analysis) was used to identify regional differences in the blood-oxygen level dependent (BOLD) signal between males and females for the following comparisons: Specific Memories versus Example Generation and Example Generation versus Riser Baseline. An additional one-sample *t*-test was performed using 3dMEMA to compare the BOLD response between the Specific Memories versus Example Generation condition for both sexes combined. Because the only behavioral differences found between groups were for positive and negative memories the additional contrasts of Specific Positive Memories versus Positive Example Generation, Specific Negative Memories versus Negative Example Generation, and Positive Specific Memories versus Negative Specific Memories also were performed using 3dMEMA. The MEMA affords the advantage over traditional *t*-tests that each participant's contribution to the final result is based on weighting instead of equal treatment, so that a more precise beta estimate (with a higher *t*-statistic) counts more in the final group effect than a less reliable beta estimate. The significance criterion for detecting differences was set at $P_{\text{corrected}} < 0.05$ determined using 3dClustSim (cluster size > 15 voxels, thresholded at voxel $P < 0.001$).

RESULTS

Behavioral Results

Participant characteristics and general task performance are presented in Table I. Men and women did not differ in their mean age, IQ, HRSD score, or anxiety ratings ($t(38) < 1.41$, $P_s > 0.17$). Of the women who were not receiving oral contraceptive agents, equal numbers were studied in the follicular and luteal phases of the menstrual cycle. There was no significant difference between sexes in the performance accuracy on the riser detection task, the number of examples generated for the distinctly valenced categories, or the ease with which such examples were generated ($t(38) < 1.00$, $P_s > 0.32$). Additionally, no difference was found in the percent of memories recalled for each specificity type ($t(38) < 1.27$, $P_s > 0.21$).

TABLE I. Mean demographic and behavioral characteristics of the study samples

Demographics	Males	Females
Age	29.6 (7.23)	32.1 (10.1)
IQ as measured using the WASI	113 (8.44)	116 (8.97)
State anxiety	24.7 (6.37)	27.2 (5.95)
Trait anxiety	25.6 (4.10)	27.3 (4.22)
HRSD	0.25 (.55)	0.70 (1.72)
Menstrual phase		
Percent of females in follicular phase		35 [n = 7]
Percent of females in luteal phase		35 [n = 7]
Percent of females using oral contraceptives		30 [n = 6]
Control tasks		
Percent correct - Riser detection task	77.1 (17.9)	76.9 (15.2)
Number of examples positive categories	5-6 (1.16)	5-6 (0.59)
Number of examples negative categories	5-6 (1.23)	5-6 (0.89)
Number of examples neutral categories	5-6 (0.87)	5-6 (0.72)
Percent of positive examples easy to generate	88.0 (13.6)	89.8 (9.78)
Percent of negative examples easy to generate	83.0 (12.6)	84.7 (14.0)
Percent of neutral examples easy to generate	88.0 (12.8)	88.7 (12.6)
Memory type		
Specific	60.3 (13.4)	61.7 (10.3)
Categorical	15.9 (8.12)	14.7 (5.71)
Extended	3.00 (2.39)	3.97 (3.46)
Semantic	6.65 (5.86)	7.74 (5.89)
Repeat	0.00 (0.00)	0.00 (0.00)
No memory	1.25 (2.01)	1.5 (2.41)
Can't recall post scan	12.9 (5.84)	10.6 (5.95)

Numbers in parentheses indicate one standard deviation of the mean.

HRDS, Hamilton Rating Scale of Depression; WASI, Wechsler Abbreviated Scale of Intelligence.

Properties of specific memory recall are presented in Table II. For specific memory recall, only Sex-by-Valence interaction was significant ($F(2,66) = 3.16$, $P = 0.02$). Follow-up tests revealed that females recalled more negative ($t(38) = 2.19$, $P_{\text{corrected}} = 0.04$) and fewer positive memories ($t(38) = 2.87$, $P_{\text{corrected}} = 0.01$) compared with males. There was no difference in the percentage of neutral memories recalled ($t(38) = 1.39$, $P_{\text{corrected}} = 1.00$). No other significant interactions with the variable sex were evident ($F_s(2,66) < 0.92$, $P_s > 0.41$) indicating that males and females did not differ in how arousing, vivid, or recent their AMs were, nor did any of these variables interact with the valence of the retrieved AM.

Imaging Results

In the combined sample (Table III), the mean BOLD activity was higher in the specific AM recall versus the example generation conditions in the right VLPFC, left lateral orbitofrontal cortex (part of the VLPFC), left DLPFC, medial PFC, bilateral middle temporal gyrus, amygdala, entorhinal cortex, parahippocampal gyrus, temporoparietal cortex, right precuneus, occipital lobe, bilateral caudal putamen, and bilateral cerebellum.

In the group comparison of Specific AM recall versus example generation, the females showed higher BOLD activity in the right DLPFC, left dorsal anterior insula, and right precuneus, while recalling specific AMs irrespective of valence (Table IV) while males had a decrease in BOLD activity in these regions. Similarly, the mean BOLD activity was higher in females in the right DLPFC and left transverse temporal gyrus for specific positive AM recall versus positive example generation while BOLD activity was decreased in the males for this contrast (Fig. 1a,b). In the right precuneus, females had higher BOLD activity for positive specific AM recall versus positive example generation while there was no corresponding change in the males (Fig. 1c). In the negative specific AM recall versus negative example generation contrast, the females showed higher BOLD activity in the right precuneus, right posterior cingulate cortex, left temporopolar cortex, and right amygdala (Fig. 2a-d). The higher BOLD activity in the females versus males in this condition is attributable to a significant increase in BOLD activity in the females with no corresponding change in the males.

Finally, for the positive specific vs. negative specific memory contrast (Table IV) a sex by condition interaction was evident in the right DLPFC and hippocampus. In the females the BOLD activity was increased in both the DLPFC and hippocampus under the positive AM condition compared to riser baseline condition. In contrast, in the males the BOLD activity in the DLPFC did not change significantly during positive or negative AM recall compared with baseline, whereas in the right hippocampus, males showed increased BOLD activity in response to both positive and negative AMs. No significant difference was

TABLE II. Properties of specific AMs by sex and valence

	Arousal			Vividness			Age memory occurred						AVERAGE FOR VALENCE
	Low	Medium	High	Low	Medium	High	Childhood	Adolescence	Remote		Adult: 6mo-1 year	Recent Adult	
									Adult	Adult			
Males	Positive	28.4 (19.5)	35.9 (17.9)	35.3 (20.9)	15.9 (15.3)	23.9 (13.9)	60.1 (20.3)	6.28 (5.78)	20.4 (15.5)	28.7 (14.5)	11.8 (7.00)	32.7 (18.5)	63.4 (12.7)
	Negative	22.7 (16.2)	36.6 (20.8)	40.6 (27.7)	12.7 (12.2)	28.3 (20.1)	59.1 (23.0)	13.6 (16.5)	18.5 (16.9)	34.7 (26.7)	8.67 (8.49)	25.6 (24.7)	27.3 (11.9)
	Neutral	59.9 (44.1)	25.8 (38.4)	14.3 (33.3)	13.2 (22.4)	31.2 (29.1)	52.2 (36.5)	8.05 (15.9)	18.1 (22.7)	27.4 (33.5)	4.63 (10.9)	41.9 (33.9)	9.04 (8.13)
	Average	29.1 (18.1)	35.9 (17.8)	34.9 (22.0)	14.9 (11.8)	25.6 (12.1)	59.5 (18.3)	9.10 (7.49)	19.9 (11.0)	29.6 (14.5)	10.8 (4.78)	31.2 (16.5)	
Females	Positive	24.9 (24.1)	33.6 (15.5)	41.5 (29.2)	7.33 (10.0)	22.5 (18.1)	70.2 (24.1)	5.81 (6.35)	11.9 (10.8)	25.5 (14.6)	18.7 (11.9)	38.1 (18.7)	54.2 (8.11)*
	Negative	19.5 (24.7)	28.7 (18.6)	50.1 (29.6)	10.3 (13.7)	27.0 (16.0)	62.7 (23.1)	8.31 (10.5)	19.3 (15.1)	29.1 (19.4)	10.8 (10.7)	32.3 (13.7)	34.5 (8.56)*
	Neutral	70.1 (36.7)	19.7 (26.7)	10.3 (25.7)	24.1 (28.5)	24.5 (23.4)	49.8 (30.0)	4.68 (9.39)	14.2 (5.74)	8.08 (11.9)	16.5 (18.4)	65.0 (30.4)	12.7 (8.61)
	Average	29.3 (23.2)	29.7 (11.8)	40.5 (26.5)	10.0 (10.6)	25.7 (14.1)	64.4 (20.6)	6.50 (6.03)	14.2 (10.5)	24.9 (12.2)	16.3 (9.23)	38.2 (13.6)	

Numbers in parentheses indicate one standard deviation of the mean. * Indicates a significant difference from the males at $P < 0.05$.

identified between males and females in the Example Generation versus Riser Baseline contrast.

DISCUSSION

Our results demonstrate both common and distinct neural mechanisms underlying AM recall in males and females. In the combined sample, the BOLD activity changes in the Specific AM condition versus the Example Generation control condition were observed in regions that previously had been identified as core components of the AM network [Svoboda et al., 2006], including the ventrolateral, dorsolateral, and medial PFC, amygdala, parahippocampal gyrus, entorhinal cortex, temporoparietal cortex, and cerebellum. In the same contrast, males and females differed in their BOLD responses in the right DLPFC, dorsal anterior insula, and right precuneus, with females showing greater hemodynamic activity than males in each region. Behavioral comparisons showed that the females recalled more negative AMs than the males, while the males recalled more positive AMs than the females. Notably, these behavioral differences were associated with sex differences in the fMRI data, with the females showing greater BOLD activity than the males in DLPFC, transverse

TABLE III. Increases in the hemodynamic response for specific AM recall versus example generation across males and females

Area	x, y, z^a	Cluster size ^b
L VLPFC (lateral orbitofrontal C)	−49, 31, −4	27
R VLPFC	57, 19, 18	55
L DLPFC	−41, 9, 50	266
L Dorsomedial PFC	−1, 53, 40	5,363
L Middle Temporal G	−55, −9, −10	2,232
R Middle Temporal G	57, 5, −18	2,051
R Amygdala	25, −9, −12	113
L Amygdala	−23, −7, −16	94
L Entorhinal C	−15, −11, −26	52
R Parahippocampal G	23, −33, −16	45
L Temporoparietal C	−55, −59, 22	1,425
R Temporoparietal C	49, −55, 20	1,311
R Precuneus	−1, −67, 32	4,424
L Caudal Putamen	−29, −13, 4	43
R Caudal Putamen	31, −9, 6	41
R Occipital Lobe	29, −87, −12	116
L Cerebellum	−26, −75, −40	384
R Cerebellum	27, −71, −34	207

^aCoordinates correspond to the stereotaxic array of Talairach and Tournoux [1988], and denote the distance in mm from the origin (anterior commissure), with positive x indicating right, positive y indicating anterior, and positive z indicating dorsal.

^bCluster size refers to the number of contiguous voxels for which the voxel t value corresponds to $P_{\text{corrected}} < 0.05$. For all peak clusters of activation, the t value > 3.62 . C, cortex; DLPFC, dorsolateral PFC; G, gyrus; L, left, PFC, prefrontal cortex; R, right; VLPFC, ventrolateral PFC.

TABLE IV. (a) Regions where hemodynamic activity differed significantly between male and female participants for the different contrasts performed and (b) for the Positive vs. Negative AMs contrast, where beta weights from the significant clusters within this contrast were extracted for Positive Specific AM recall vs. Riser Baseline and Negative Specific AM Recall vs. Riser Baseline

			β Weight	
Area	x, y, z	Cluster size	Males	Females
All Specific AMs vs. example generation (a)				
R DLPFC	25, 23, 42	23	−0.02 (0.01)	0.13 (0.05)
L Dorsal Anterior Insula	−33, 3, 12	20	−0.05 (0.02)	0.12 (0.02)
R Precuneus	5, −51, 62	17	−0.04 (0.02)	0.10 (0.02)
Positive Specific AMs vs Positive Example Generation				
R DLPFC	25, 23, 40	15	−0.03 (0.01)	0.12 (0.05)
L Transverse Temporal G	−41, −25, 10	15	−0.12 (0.03)	0.05 (0.02)
R Precuneus	3, −69, 38	18	0.07 (0.08)	0.47 (0.11)
Negative Specific AMs vs Negative Example Generation				
R Posterior Cingulate C	5, −19, 38	15	−0.01 (0.02)	0.17 (0.05)
L Temporopolar C	−51, 11, −18	26	0.02 (0.04)	0.26 (0.07)
R Precuneus	5, −51, 62	15	−0.01 (0.02)	0.17 (0.05)
R Amygdala	31, −9, −14	21	0.01 (0.02)	0.15 (0.04)

			β Weight			
			Males		Females	
Area	x, y, z	Cluster Size	Positive AMs	Negative AMs	Positive AMs	Negative AMs
Positive specific AMs vs. negative specific AMs (b)						
R DLPFC	25, 13, 42	21	−0.02 (0.02)	0.01 (0.02)	0.07 (0.04)	0.03 (0.03)
R Hippocampus	35, −15, −24	22	0.06 (0.03)	0.09 (0.03)	0.10 (0.03)	−0.01 (0.02)

Numbers in parentheses indicate one standard deviation of the mean. Coordinates, cluster size and abbreviations correspond to those in Table III. For all peak clusters of activation, the t value > 3.54 , corresponding to $P_{\text{corrected}} < 0.05$. C, cortex; DLPFC, dorsolateral PFC; G, gyrus; L, left; OFC, orbitofrontal cortex; R, right.

temporal gyrus, and precuneus in the Positive Specific AM vs. Positive Example Generation contrast, and in the posterior cingulate, temporopolar cortex, precuneus, and amygdala in the Negative Specific AM vs. Negative Example Generation contrast. Additional sex differences in BOLD activity were evident in the DLPFC and hippocampus when directly comparing the Positive and Negative AM Recall conditions. Consistent with previous neuroimaging studies of sex differences in AM recall [Piefke, et al., 2005; St Jaques et al., 2010], the groups did not differ significantly in other properties of these memories (vividness, arousal, age of occurrence).

Several of the areas where females exhibited greater hemodynamic activity than males have been implicated in tasks assessing cognitive control [Levesque et al., 2003], the development of empathy [Hooker et al., 2010] or the processing of emotions [Maddock et al., 2002]. When recalling specific AMs, and especially positive specific AMs, females showed greater BOLD activity than males in the right DLPFC. This area showed greater BOLD activity for AM recall compared to the checkerboard detection

baseline in females than males in the study by Piefke et al. [2005], although the specific area where hemodynamic activity increased in this study was located anterior to that found by Piefke et al. [2005]. The DLPFC is involved in a variety of cognitive domains, including the processing of the temporal context of memory [Suzuki et al., 2002] and the suppression of emotional reactions [Levesque et al., 2003]. Although Piefke et al. [2005] interpreted their findings of increased DLPFC activity in females as evidenced that females implement temporal sequencing of their memories to a greater extent than males, an alternative explanation conceivably may be that the increased activity in this region in females indicates relatively greater engagement of cognitive control to minimize intense emotional responses.

In the left transverse temporal gyrus the significant sex by task interaction was attributable to a decrease in the BOLD signal during positive specific AMs relative to positive example generation in the males with no corresponding change in the females. This region is in the vicinity of the primary auditory cortex [Binder et al., 1994]. Since

Figure 1.

Left panel: Regions where females showed increased hemodynamic activity versus males while recalling emotionally positive, specific autobiographical memories relative to generating examples of positive categories, depicted as voxel t -values corresponding to $P_{\text{corrected}} < 0.05$ superimposed on the template anatomical MRI sections. Right panel: The mean ($\pm$ SEM) beta

weights associated with each adjacent image as measured over (a) the right DLPFC at $x, y, z = 25, 23, 40$, (b) the left transverse temporal gyrus at $x, y, z = -41, -25, 10$, and (c) the right precuneus at $x, y, z = 3, -69, 38$. Coordinates interpreted as indicated in the legend for Table III.

Figure 2.

Regions where females showed an increased hemodynamic activity during negative specific autobiographical memory recall compared to negative example generation ($P_{\text{corrected}} < 0.05$) and the associated beta weights for the (a) right posterior cingulate at $x,$

$y, z = 5, -19, 38$ (b) left temporopolar cortex at $x, y, z = 51, 11, -18$ (c) right precuneus at $x, y, z = 5, -51, 62$ and (d) right amygdala at $x, y, z = 31, -9, -14$. Coordinates interpreted as indicated in the legend for Table III.

greater selective attention is often associated with suppression of activity in cross-modal sensory regions [Drevets et al., 1995; Haxby et al., 1994; Roland, 1982], the lack of suppression in this region in females conceivably may relate to why they were less successful than males in recalling positive AMs. Males potentially may be more attentionally engaged during the processing of positive emotional mnemonic cues than females.

When recalling negative specific AMs, females showed greater hemodynamic activity compared with males in the right posterior cingulate cortex, temporopolar cortex, and amygdala. All three areas participate in an extended “visceromotor network” with medial PFC structures that is involved in processing and modulating the visceral aspects of emotional behavior [Price and Drevets, 2010]. The posterior cingulate cortex is involved in processing emotional information and may mediate interactions between emotional and memory-related processes [Maddock et al., 2002]. The amygdala is involved with responses to fearful and sad stimuli, and stimulation of the amygdala produces autonomic reactions and freezing behavior in experimental animals, and feelings of fear and anxiety in humans [Ledoux, 1996]. Additionally, sex differences in autonomic responding to cognitive stressors differentially activates the amygdala in males and females [Nugent et al., 2011], such that females showed a positive correlation between amygdala responses and heart rate variability, suggesting the increased amygdala activity seen in females in this study is related to engagement of emotional control. Interestingly, both the posterior cingulate and amygdala show increased glucose metabolism under resting conditions in samples with major depressive disorder [MDD; Price and Drevets, 2010]. The greater recruitment of these areas in healthy females relative to healthy males suggests the hypothesis that sex differences in the processing of negative versus positive information may contribute to the greater risk for developing MDD in females than in males [Wright et al., 2009]. The temporal pole, also found to be more active in females than males during specific negative AM recall, shares extensive, reciprocal anatomical projections with the amygdala [Olson et al., 2007; Price and Drevets, 2010]. The temporopolar cortex also has been implicated in theory of mind tasks and feelings of empathy [Olson et al., 2007].

Sex differences were evident in the BOLD response of the right hippocampus when the positive and negative specific AM recall conditions were compared directly. In males, the hippocampal BOLD signal increased during both positive and negative AM recall. In the females, however, the hippocampal BOLD signal increased during positive, but not negative, AM recall. In a previous study activity within the right hippocampus correlated with memory vividness [Gilboa et al., 2004]. The finding that females activated the hippocampus to the same extent as the males during positive AM recall while only the males activated this region during negative AM recall raises the hypothesis that females may have engaged cognitive cir-

cuits involved in affective modulation in order to control to attenuate the intensity of negative AMs. Differential activation in this region between males and females during negative AM recall extends previous reports by Piefke et al. [2005] and St Jacques et al. [2010] that men showed greater activity than women in the hippocampus or parahippocampus during AM recall (irrespective of valence).

The BOLD activity was higher in the dorsal anterior insula in the females relative to the males as they recalled specific AMs, but did not show differential activation between the sexes in the contrasts examining emotional valence. Hemodynamic activity increases in this subregion of the insula under a range of experimental conditions, which have included during the experience of and reflection upon negative emotions [Carr et al., 2003], and the experience of empathy and compassion [Lamm and Singer, 2010].

Finally, the females showed greater BOLD activity than the males in the right precuneus during specific AM recall, irrespective of the valence of the AMs. This region is involved in self-referential processing and taking on a first person perspective [Cavanna and Trimble, 2006]. The precuneus is an important area for both the consolidation and retrieval of AMs; and more particularly, for specific AM recall versus general memory recall [Addis et al., 2004].

Taken together, our results would appear to be more supportive of the cognitive styles hypothesis rather than the affect intensity hypothesis of AM retrieval. The affective intensity hypothesis would predict women have higher ratings of AM arousal than males, differences that were not present in the current study. Specifically, while the females retrieved more negative AMs than the males, in association with increased activity in the amygdala, the vividness and arousal associated with these memories at the time of recall did not differ between groups. Our results instead suggest females may employ different cognitive strategies than males, possibly in association with a greater engagement of cognitive control over their emotional response, as reflected by increased activity in the DLPFC, superior temporal gyrus, and posterior cingulate cortex.

Additionally, the sex differences observed in the hemodynamic responses of the dorsal anterior insula and temporopolar cortex are noteworthy in that these regions have been implicated in the experience of empathy [Lamm and Singer, 2010; Olson et al., 2007], and women are reportedly more empathetic than men [Mestre et al., 2009]. As empathy involves feelings towards others, it may be the case that women have more social memories involving other people than men. Our experimental design did not address this question; however, as we did not collect data regarding empathic feeling in our participants or concerning whether the cued memories involved self only or other people as well. Future studies of sex differences in AM recall should include measures of empathy and self/other orientation of AMs to further examine these constructs and how they may relate to sex differences in AM recall.

Our results are consistent with those of Piefke et al. [2005] insofar as we did not find differences in the emotional intensity of the recalled memories between sexes, yet did detect differences in the hemodynamic responses of prefrontal and insular cortices. Our findings that females recalled more negative and fewer positive AMs are not necessarily in conflict with Piefke et al. [2005] as they collected memories prior to scanning and then selected an equivalent number of positive and negative memories. Piefke et al. [2005] did not assess differences in the number of distinctly valenced memories between males and females, but instead investigated whether differences in the properties of those memories existed between sexes. St Jacques et al. [2010] also did not examine differences in the numbers of distinctly valenced memories, but only in their phenomenological properties. Therefore, our behavioral results are similar to those reported in previous imaging studies of sex differences in AM recall in that we also did not find differences in the properties (such as vividness or arousal) of the AMs recalled by participants.

Some differences between the methods employed in the current study and that of Piefke et al. [2005] and St Jacques et al. [2010] merit comment. First, our sample sizes were about twice as large as those studied by Piefke et al. [2005] and St Jacques et al. [2010], so the differences in the results across studies are less likely to reflect Type II error in the results from our study. Instead the fundamental design differences in the memory task between our study and these previous studies may more likely account for their distinct results. Both previous studies used a recognition paradigm of AM retrieval where AMs were collected prior to the scan and, whereas our study used a pure recall paradigm where AMs were generated during scanning. The differences in neural activity elicited by our AM recall task and the memory task used in these other studies may account for this difference in their results. Recalling, as opposed to recognizing AMs, may have resulted in the temporal lobe and precuneus activation found in this study.

One limitation of our design that merits comment is that we did not limit scanning of the female participants to a specific phase of the menstrual cycle, and did not have sufficient power to further analyze either the behavioral or neuroimaging data by menstrual phase. Differences have been found in memory recall and neural processing across menstrual phases in females. For example, the BOLD response to negatively valenced pictures in the amygdala and medial temporal lobe structures differs between women in the mid-luteal and early follicular phases [Andreano and Cahill, 2010; Van Wingen et al., 2011], sex differences between the BOLD response to negatively valenced stimuli are most pronounced during the luteal phase [Goldstein et al., 2010], and memory for emotional pictures is increased during the luteal compared with follicular phase [Ertman et al., 2011]. Because we had an equivalent number of women in the follicular and luteal

phases as well as of women using hormonal contraception, our results are indicative of an overall sex difference, irrespective of menstrual status. However, our results may not generalize to samples studied in only a single phase.

Another potential limitation of our study design is that the entire 12 second window following cue presentation was analyzed and therefore, at least some portion of the response can be attributed to affective processing of the cue word. Because it was not possible to determine precisely when mnemonic processing commenced in the epoch that immediately followed cue presentation, it was necessary to include the entire period. Although some portion of the response would be attributable to affective processing, this type of processing presumably would have occurred for both the example generation and memory conditions, as both cue words were matched for valence, arousal, vividness, and frequency of use in the English language. The lack of sex differences in the BOLD response during the example generation condition thus supports the conclusion that the observed differences during AM recall were in fact related to the process of searching for and recalling an AM as opposed to differences in affective processing.

The results of this study converge with those of previous studies to support the existence of sex differences in AM recall and to define the functional anatomical correlates of these differences. The extant data further appear to support the hypothesis that such differences depend on dissimilar cognitive strategies of encoding, rehearsing, and/or ruminating about past experiences.

ACKNOWLEDGMENTS

The research described herein was performed at the Laureate Institute for Brain Research. The funders had no role in study design, data, collection, analysis, decision to publish, or preparation of this manuscript. The authors had full access to all of the data in the study and take responsibility for the integrity of the data and the accuracy of the data analysis. The authors have no conflict of interest to declare.

REFERENCES

- Addis DR, Moscovitch M, Crawley AP, McAndrews MP (2004): Recollective qualities modulate hippocampal activation during autobiographical memory retrieval. *Hippocampus* 14:752–762.
- Anderson R, Goddard L, Powell J (2009): Reduced specificity of autobiographical memory as a moderator of the relationship between daily hassles and depression. *Cogn Emot* 24:704–709.
- Andreano JM, Cahill L (2009): Sex influences on the neurobiology of learning and memory. *Learn Mem* 16:2260–2671.
- Andreano JM, Cahill L (2010): Menstrual cycle modulation of medial temporal activity evoked by negative emotion. *Neuroimage* 53:1286–1293.
- Binder JR, Rao SM, Hammeke TA, Yetkin FZ, Jesmanowicz A, Bandettini PA, Wong EC, Estowski LD, Goldstein MD,

- Haughton VM (1994): Functional magnetic resonance imaging of human auditory cortex. *Ann Neurol* 35:662–672.
- Bradley MM, Lang PJ (1999): Affective Norms for English Words (ANEW). The NIMH Center for the Study of Emotion and Attention, University of Florida: Gainesville, FL.
- Cabeza R, Prince SE, Daselaar SM, Greenberg DL, Buddle M, Dolcos F, LaBar KS, Rubin DC (2004): Brain activity during episodic retrieval of autobiographical and laboratory events: An fMRI study using a novel photo paradigm. *J Cogn Neurosci* 16:1583–1594.
- Carr L, Iacoboni M, Dubeau MC, Mazziotta JC, Lenzi GL (2003): Neural mechanisms of empathy in humans: A relay from neural systems for imitation to limbic areas. *Proc Natl Acad Sci USA* 100:5497–5502.
- Cavanna AE, Trimble MR (2006): The precuneus: A review of its functional anatomy and behavioral correlates. *Brain* 129:564–583.
- Conway MA (1992): A structural model of autobiographical memory. In: Conway MA, Rubin DC, Spinnler H, Wagenaar WA, editors. *Theoretical Perspectives on Autobiographical Memory*. Dordrecht: Kluwer Academic Publishers. pp. 167–194.
- Conway MA, Turk DJ (1999): A positron emission tomography (PET) study of autobiographical memory retrieval. *Memory* 7:679–702.
- Conway MA, Pleydell-Pierce CW, Whitecross SE, Sharpe H (2002): Neurophysiological correlates of memory for experienced and imagined events. *Neuropsychologia* 41:334–340.
- Davis PJ (1999): Sex differences in autobiographical memory for childhood emotional experiences. *J Pers Soc Psychol* 76:379–386.
- Denkova E, Botzung A, Scheiber C, Manning L (2006): Implicit emotion during recollection of past events: A nonverbal fMRI study. *Brain Res* 1078:143–150.
- Drevets WC, Burton H, Videen TO, Snyder AZ, Simpson JR Jr, Raichle ME (1995): Blood flow changes in human somatosensory cortex during anticipated stimulation. *Nature* 373:249–252.
- Ertman N, Andreano M, Cahill L (2011): Progesterone at encoding predicts subsequent emotional memory. *Learn Mem* 18:759–763.
- Fink GR, Markowitsch HJ, Reinkemeier M, Bruckbauer T, Kessler J, Wolf-Dieter H (1996): Cerebral representation of one's own past: Neural networks involved in autobiographical memory. *J Neurosci* 16:4275–4282.
- First MB, Spitzer RL, Gibbon M, Williams JBW (2002): *Structured Clinical Interview for DSM-IV-TR Axis I Disorders, Research Version, Patient Edition (SCID-I/P)*. New York State Psychiatric Institute, Biometrics Research: New York, NY.
- Fujita F, Diener E, Sanvik E (1991): Sex differences in negative affect and well-being: The case for emotional intensity. *J Pers Soc Psychol* 61:427–434.
- Gardini S, Cornoldi C, De Beni R, Venneri A (2006): Left medio-temporal structures mediate the retrieval of episodic autobiographical mental images. *Neuroimage* 30:645–655.
- Gilboa A, Wincour G, Grady CL, Hevenor SJ, Moscovitch M (2004): Remembering out past: Functional neuroanatomy of recollection of recent and very remote personal events. *Cereb Cortex* 14:1214–1225.
- Goldstein JM, Jerram M, Abbs B, Whitfield-Gabrieli S, Makris N (2010): Sex differences in stress response circuitry activation dependent on female hormone cycle. *J Neurosci* 30:431–438.
- Hamilton M (1960): A rating scale for depression. *J Neurol Neurosurg Psychiatry* 23:56–62.
- Haxby JV, Horowitz B, Underleider LG, Maisog JM, Pietrini P, Grady CL (1994): The functional organization of human extrastriate cortex: A PET-rCBF study of selective attention to faces and locations. *J Neurosci* 14:6336–6353.
- Hooker CL, Verosky SC, Germine LT, Knight RT, D'Esposito M (2010): Neural activity during social signal perception correlates with self-reported empathy. *Brain Res* 1308:100–113.
- Lamm C, Singer T (2010): The role of anterior insular cortex in social emotions. *Brain Struct Funct* 241:579–591.
- Ledoux J (1996): Emotional networks and motor control: A fearful view. *Prog Brain Res* 107:437–446.
- Levesque J, Eugene F, Joanne V, Paquette V, Mensour B, Beaudoen G, Leroux JM, Bourgoin P, Beauregard M (2003): Neural circuitry underlying voluntary suppression of sadness. *Biol Psychiatry* 53:502–510.
- Levine B, Turner GR, Tisserand D, Hevenor SJ, Graham SJ, McIntosh AR (2004): The functional neuroanatomy of episodic and semantic autobiographical remembering: A prospective functional MRI study. *J Cogn Neurosci* 16:1633–1646.
- Maddock RJ, Garrett AS, Buonocore MH (2002): Posterior cingulate cortex activation by emotional words: fMRI evidence from a valence distraction task. *Hum Brain Mapp* 18:30–41.
- Maguire EA, Henson RNA, Mummery CJ, Frith CD (2001): Activity in the prefrontal cortex, not hippocampus, varies parametrically with the increasing remoteness of memories. *NeuroReport* 12:441–444.
- Maguire EA, Frith CD (2003): Aging affects the engagement of the hippocampus during autobiographical memory retrieval. *Brain* 126:1511–1523.
- Maxwell ME (1992): *Family Interview for Genetic Studies (FIGS): manual for FIGS*. Bethesda, MD: National Institute of Mental Health, Clinical Neurogenetics Branch, Intramural Research Program.
- Mestre MV, Samper P, Frias MD, Tur AM (2009): Are women more empathetic than men? A longitudinal study in adolescence. *Span J Psychol* 12:76–83.
- Nugent AC, Bain EE, Thayer JF, Sollers JJ, Drevets WC (2011): Sex differences in the neural correlates of autonomic arousal: A pilot PET study. *Int J Psychophysiol* 80:182–191.
- Olson IR, Plotzker A, Ezzyat Y (2007): The enigmatic temporal pole: A review of findings on social and emotional processing. *Brain* 130:1718–1731.
- Piefke M, Weiss PH, Zilles K, Markowitsch HJ, Fink GR (2003): Differential remoteness and emotional tone modulate the neural correlates of autobiographical memory. *Brain* 126:650–668.
- Piefke M, Weiss PH, Markowitsch HJ, Fink GR (2005): Sex differences in the functional neuroanatomy of emotional episodic autobiographical memory. *Hum Brain Mapp* 24:313–324.
- Price JL, Drevets WC (2010): Neurocircuitry of mood disorders. *Neuropsychopharmacology* 35:192–216.
- Roland PE (1982): Cortical regulation of selective attention in man: A regional cerebral blood flow study. *J Neurophysiol* 48:1059–1078.
- Rubin DC, Schulkind MD, Rahhal TA (1999): A study of sex differences in autobiographical memory: Broken down by age and sex. *J Pers Soc Psychol* 74:262–271.
- Ryan L, Nadel K, Keil K, Putnam K, Schnyer D, Trouard T, Moscovitch M (2001): Hippocampal complex and retrieval of recent and very remote autobiographical memories: Evidence from functional magnetic resonance imaging in neurologically intact people. *Hippocampus* 11:707–714.
- Seidltz L, Diener E (1998): Sex differences in the recall of affective experiences. *J Pers Soc Psychol* 74:262–271.

-
- Skudlarski P, Constable RT, Gore JC (1999): ROC analysis of statistical methods used in functional MRI: Individual subjects. *NeuroImage* 9:311–329.
- Spielberger CD, Gorsuch RL, Lushene PR, Vagg PR, Jacobs AG (1983): *Manual for the State-Trait Anxiety Inventory (Form Y)*: Consulting Psychologists Press: Palo Alto.
- St Jacques P, Conway MA, Cabeza R (2010): Sex differences in autobiographical memory for everyday events: Retrieval elicited by SenseCam images versus verbal cues. *Memory* 19:723–732.
- Suzuki M, Fujii T, Tsukiura I, Takahashi S, Yamadori A (2002): Neural basis of temporal context memory: A functional MRI study. *Neuroimage* 17:1790–1796.
- Svoboda E, McKinnon M, Levine B (2006): The functional neuroanatomy of autobiographical memory: A meta-analysis. *Neuropsychologia* 44:2189–2208.
- Talairach J, Tournoux P (1988): *Co-planar Stereotaxic Atlas of the Human Brain: 3-Dimensional Proportional System—An Approach to Cerebral Imaging*. New York: Thieme Medical Publishers.
- Tulving E (2002): Episodic memory: from mind to brain. *Annu Rev Psychol* 53:1–25.
- Van Wingen GA, Ossewaarde L, Backström T, Hermans EJ, Fernandez G (2011): Gonadal hormone regulation of the emotion circuitry in humans. *Neuroscience* 191:38–45.
- Wechsler D (1999): *Wechsler Abbreviated Scale of Intelligence (WASI)*. San Antonio, TX: Harcourt Assessment.
- Williams JM, Broadbent K (1986): Autobiographical memory in suicide attempters. *J Abnormal Psychol* 95:144–149.
- Williams J, Scott J (1988): Autobiographical memory in depression. *Psychol Med* 18:689–695.
- Williams J, Barnhofer T, Crane C, Hermans D, Raes F, Watkins E, Dalgleish T (2007): Autobiographical memory specificity and emotional disorder. *Psychol Bull* 133:122–148.
- Wright SL, Langenecker SA, Deldi PJ, Rappor LJ, Nielson KA, Kade AM, Own LS, Akil H, Young EA, Zubieta JK (2009): Sex-specific disruptions in emotion processing in younger adults with depression. *Depress Anxiety* 26:182–189.