Does Sleep Promote False Memories?

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Abstract

■ Memory is constructive in nature so that it may sometimes lead to the retrieval of distorted or illusory information. Sleep facilitates accurate declarative memory consolidation but might also promote such memory distortions. We examined the influence of sleep and lack of sleep on the cerebral correlates of accurate and false recollections using fMRI. After encoding lists of semantically related word associates, half of the participants were allowed to sleep, whereas the others were totally sleep deprived on the first postencoding night. During a subsequent retest fMRI session taking place 3 days later, participants made recognition memory judgments about the previously studied associates, critical theme words (which had not been previously presented during encoding), and new words unrelated to the studied items. Sleep, relative to sleep deprivation, enhanced accurate and false recollections. No significant difference was

observed in brain responses to false or illusory recollection between sleep and sleep deprivation conditions. However, after sleep but not after sleep deprivation (exclusive masking), accurate and illusory recollections were both associated with responses in the hippocampus and retrosplenial cortex. The data suggest that sleep does not selectively enhance illusory memories but rather tends to promote systems-level consolidation in hippocampo-neocortical circuits of memories subsequently associated with both accurate and illusory recollections. We further observed that during encoding, hippocampal responses were selectively larger for items subsequently accurately retrieved than for material leading to illusory memories. The data indicate that the early organization of memory during encoding is a major factor influencing subsequent production of accurate or false memories. ■

INTRODUCTION

Declarative memory is our ability to recollect everyday events and factual knowledge (e.g., Eichenbaum, 2000). Memories can vary according to several descriptive features, including the relation to the memory of a specific context and a mode of retrieval. That is, remembering and knowing are states of awareness that accompany the retrieval of experiences from our past determining whether participants recollect (i.e., "Remembering") their memories or used a rough feeling of familiarity (i.e., "Knowing") to base their decision. Imaging studies have shown that information that is later remembered is specifically associated with hippocampal responses (e.g., Davachi & Wagner, 2002). Of particular interest for the current study, our memories are interconnected associations constituting a record of our personal experiences that is continuously updated

(i.e., new information is continuously reorganized within the context of previous knowledge). Hence, when we remember a specific episode, related associations or connected concepts might also come to mind. Consequently, our memories are not literal records of past events. What is retrieved from memory can substantially differ from the actual episode due to distortion or addition of various details (Schacter, 1999; Bartlett, 1932). False memories are good examples of such memory distortions, during which an event is remembered, although in actual fact, it never happened (Roediger & McDermott, 1995). As a rule, such false memories are strongly semantically associated to the actually encoded items (Schacter, 1996). The "Deese–Roediger–McDermott" (DRM) paradigm capitalizes on these strong semantic relationships to reliably elicit high proportions of false memories. In this paradigm, participants learn word lists that compile semantically associated words, except the strongest associate, the theme of the list. The latter has high probability to be subsequently incorrectly retrieved as a critical lure. Besides the structure of the learned material, a number of factors influence the formation of false memories during both encoding and retrieval (Gallo, 2006). In

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addition, like their veridical counterparts, false memories seem to undergo a consolidation process. Over time, false memories become increasingly resistant and even persist better than veridical memories (Seamon et al., 2002; Mc Dermott, 1996; Reyna & Brained, 1995).

Sleep has been shown to promote the consolidation of declarative memory (Rasch & Born, 2007). The sleep-dependent off-line processing of recent memories would entail not only the adaptation of synaptic strength to maintain synaptic homeostasis (Tononi & Cirelli, 2006) but also the macroscopic reorganization within cerebral networks (Albouy et al., 2008; Gais et al., 2007; Sterpenich et al., 2007; Orban et al., 2006). In particular, for hippocampal-dependent memories, the burden of retention is thought to be progressively transferred from hippocampal to neocortical stores. This process would particularly involve an interplay between the hippocampus and the mesial prefrontal areas (Frankland & Bontempi, 2005), the activity of which grows progressively at retrieval as the interval because encoding increases (Sterpenich et al., 2007, 2009; Gais et al., 2007; Takashima et al., 2006).

Importantly, there is evidence that sleep does not promote only the consolidation of declarative memories but can lead to behavioral modifications that entail the generation during sleep of novel representations on the basis of information extracted from learned exemplars (Ellenbogen, Hu, Payne, Titone, & Walker, 2007; Wagner, Gais, Haider, Verleger, & Born, 2004). Similarly, false memories are suggested to arise from the activation by studied words of other semantically related representations, including the critical lure (Roediger, Watson, McDermott, & Gallo, 2001). Alternatively, false memory would imply the extraction of the gist of the memory from the studied word lists (Brainerd & Reyna, 2002). Collectively, these experimental and theoretical elements raise the possibility that sleep might also promote the formation of false memories.

At present, this hypothesis has received mixed experimental support. One study using the DRM paradigm reported that false, in contrast to veridical, recall is better preserved after (both nocturnal and diurnal) sleep than after equivalent periods of wakefulness (Payne et al., 2009). In contrast, in another study also based on DRM, the proportion of false recognitions was not changed after sleep but was enhanced only by sleep deprivation immediately preceding retrieval (Diekelmann, Landolt, Lahl, Born, & Wagner, 2008).

Here, we used fMRI and DRM paradigm to investigate the influence of sleep and lack of sleep during the post-encoding night, on the neural correlates of veridical and illusory recollection, that is, memory retrieval processes accompanied by the recovery of specific contextual details. We found that sleep had only a moderate effect on the proportion of false recognitions and modified their neural correlates to the same extent as accurate memories. We further show that in contrast, response patterns elicited during encoding of the material significantly influence the subsequent production of false recognitions.

METHODS

Participants

Thirty-six young, native French speaking, healthy volunteers (23 women, mean age = 22.3 ± 2.7 years) were recruited by advertisement. They gave their written informed consent to take part in this fMRI study, which was approved by the ethics committee of the Faculty of Medicine of the University of Liège. They received a financial compensation for their participation. Semistructured interviews established the absence of medical, traumatic, psychiatric, or sleep disorders. All participants were nonsmokers, were moderate caffeine and alcohol consumers, and were not on medication. They were right-handed as indicated by the Edinburgh Inventory (Oldfield, 1971). The quality of their sleep was normal as assessed by the Pittsburgh Sleep Quality Index questionnaire (Buysse, Reynolds, Monk, Berman, & Kupfer, 1989). None complained of excessive daytime sleepiness as assessed by the Epworth Sleepiness Scale (Johns, 1991). Extreme morning and evening types as determined by the Horne–Ostberg Questionnaire (Horne & Ostberg, 1976) were not included. All participants had normal scores at the 21-item Beck Anxiety Inventory, the 21-item Beck Depression Inventory II. The self-assessed scores for depression, anxiety, alexithymia, sleepiness, sleep quality, and circadian rhythms and age did not revealed any significant difference in sleep-deprived (SD) and sleep nondeprived (S) groups ($p > .5$).

Experimental Design

Volunteers followed a 7-day constant sleep schedule (according to their own circadian rhythm ± 1 hr) before the first visit and kept the same schedule for three more days until their second visit. Compliance to the schedule was assessed during the preceding week, using wrist actigraphy (Cambridge Neuroscience, Cambridge, UK) and sleep diaries. Volunteers were requested to refrain from all caffeine and alcohol-containing beverages 1 week before participating in the study.

Each subject was scanned during two separate fMRI sessions (Figure 1). Following the DRM paradigm, during the first session (encoding, between 6:30 and 8:30 p.m.), participants listened to a set of 32 auditorily presented thematic lists, each of which consisted 15 semantic associates (i.e., a total of 480 target items) converging to a critical nonpresented theme word (lure). Each of the lists was controlled and selected in a previous behavioral study in which participants strongly tended to falsely recall or recognize these critical lures (unpublished data). Each list was recorded using SoundEdit resource files by a female speaker, and the interval between the presentation of two words was 2000 msec. Words were presented in order of decreasing strength of association to the theme word. Participants were instructed to listen carefully to each list and to try to remember the words in preparation for a later test. They were not informed of the specific nature
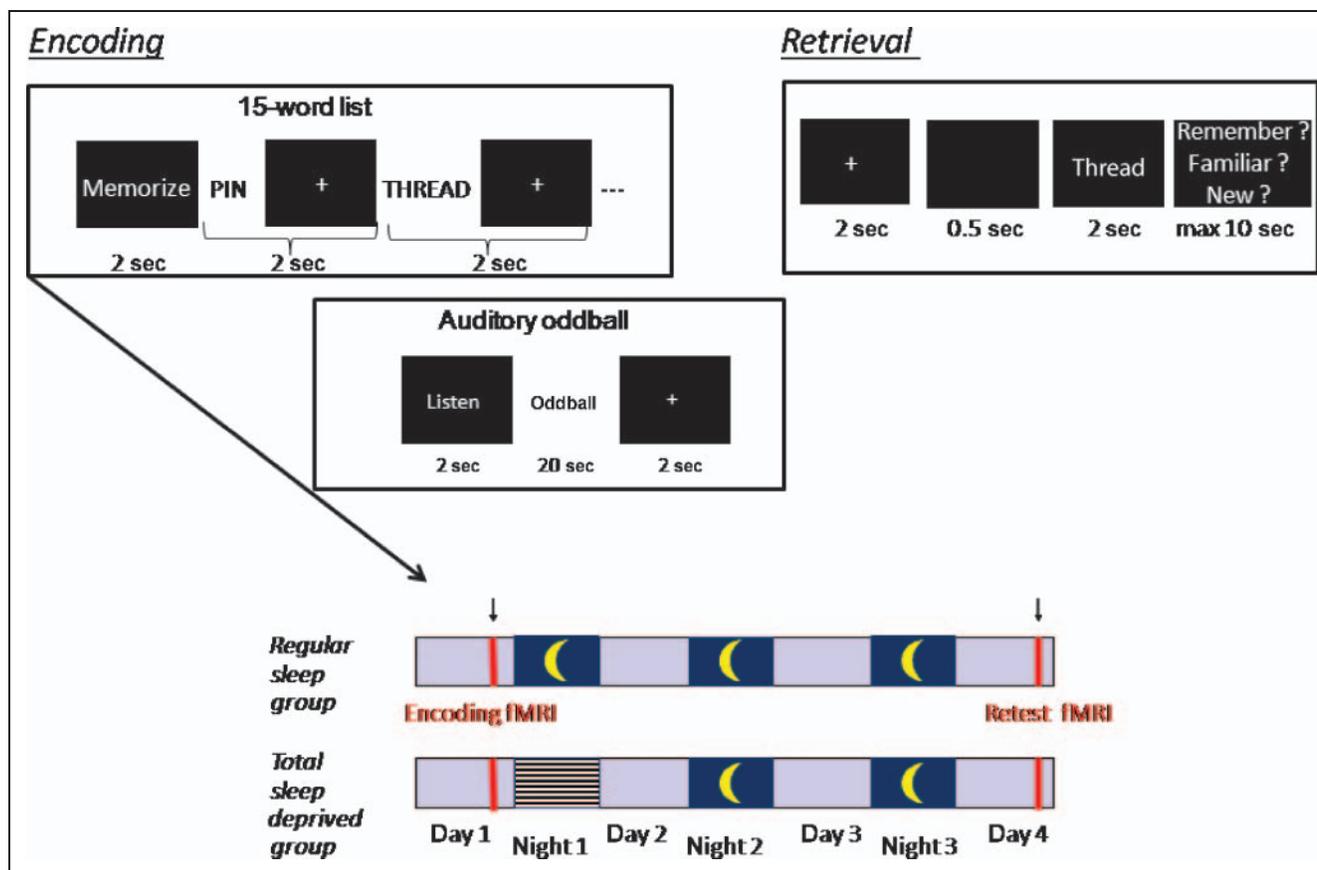
Figure 1. Experimental design.

and modality of the recognition test. During the data acquisition period, all participants interacted with the same investigator who used a standardized set of sentences to minimize social interferences. To minimize the rehearsal process, we separated the presentation of each of the 32 lists by a 20-sec interval, during which participants completed an oddball task. Participants were required to count the odd tones and to respond to them by pressing a key as fast as possible. Ten auditory stimuli per oddball task were presented, consisting of frequent (600 Hz) and odd tones (400 Hz). The first three auditory stimuli were always frequent tones; the others were presented in pseudorandomized order. Each tone was 600 msec long, with an SOA of 2000 msec. Tones and words were delivered with COGENT2000 (http://www.vislab.ulc.ac.uk/Cogent/) and were transmitted to the participants by using MR CONTROL audio system (MR Confon, Germany). The volume level of both tones and words was set by the volunteer before the session.

Participants were pseudorandomly assigned to two groups according to whether they were allowed to sleep (S, $n = 18$, 12 women, mean age = 22.6 ± 3.0 years) or were totally sleep deprived (SD, $n = 18$, 11 women, mean age = 21.9 ± 3.8 years) during the first postencoding night. In the S group, participants went home after the encoding session and slept regularly as during the week before during the three postencoding nights. In the SD group, the participants stayed awake in the laboratory during the first postencoding night (from 11:00 p.m. to 7:00 a.m.). During this night, the participants remained under the constant supervision of experimenters, and their physical activity was maintained as low as possible. Light was kept under 30 lux. Every hour, participants were allowed to stand up and to eat a small calibrated snack. These measures aimed at decreasing the physiological stress inherent to sleep deprivation procedures (Meerlo, Sgoifo, & Suchecki, 2008). During the following day, participants were instructed to continue their usual activities. They slept at home during the two remaining nights. Participants were informed of their attribution to SD or S group only after the end of the encoding session. Pseudorandom assignment to S or SD groups was specified by the day of the encoding session.

The retest session took place between 3:30 and 5:30 p.m., after two recovery nights, and consisted of a remember/know/new judgment on the target items, lures, and new words. During this recognition task, participants had to classify 10 items per list as either previously studied (word listened) or unstudied: (i) four words from each of the 32 lists that had actually been listened during learning (in Positions 1, 4, 8, and 12 of a list; later referred to as old items [O]); (ii) four semantically unrelated distractor words matched in terms of length, gender, frequency, and imageability to the four studied words (DS); (iii) the

critical theme word (lure; L); and (iv) the semantically unrelated distractor word matched to the critical theme word (DL). In total, 320 words were presented in random order, including 128 studied words, 32 lures, and 160 new words.

Each word was displayed for 2000 msec at the center of the screen, and participants had a maximum of 10,000 msec to choose one of three possible choices: "Remember," "Know," or "New." A "Remember" response indicated that the recognition of the item was associated with retrieval of specific contextual details during encoding (e.g., the order in the list or the pronunciation). A "Know" response was associated with the feeling of having encoded the item but without being able to retrieve any further specific details. The instructions given for these judgments were based on those provided by Tulving (1985). "Remember" responses indicated a specific recollection about the item (i.e., episodic retrieval), whereas "Know" responses were given when participants had no specific recollection of the item's occurrence but believed that the item had been in the list (i.e., a familiarity response based on semantic processing). A "New" response was given when the participant thought the item had not been presented during encoding. Participants gave their responses on a three-button keypad that they held in their right hand.

Behavioral Analysis

Statistical analyses consisted of two-way ANOVAs on the groups of S and SD participants. A statistical level of $p < .05$ was used for all analyses. When significant effects were observed, planned comparisons were next performed, also with a statistical level of $p < .05$. Overall recognition performance (R + K responses), recollection (R responses) and familiarity (K responses) processes were compared for studied items, distracters, and lures.

Actigraphic Data Analysis

Actigraphy data were analyzed for the three nights between the encoding and the retest session. The bounds of the nights were estimated as a period of decrease in movements. For the deprivation night, mean of movements was estimated from 11:00 p.m. to 7:00 a.m., corresponding to the period during which participants stayed awake in the laboratory. We performed a repeated measure ANOVA with mean of movements for three periods of night (first night of sleep or sleep deprivation, second night, and third night before retest) as within-subject factors and sleep (SD vs. S) as between-subject factor. Planned comparison tested the difference between both groups for the three nights separately.

fMRI Data Analysis and Scan Acquisition

Functional MRI time series were acquired using a 3-T Allegra MR scanner (Siemens, Erlangen, Germany). Multislice T2*-weighted fMRI images were obtained with a gradient-echo-planar sequence using axial slice orientation (32 transverse slices; voxel size = 3.4 × 3.4 × 3 mm^3; matrix size = 64 × 64 × 32; repetition time = 2130 msec; echo time = 40 msec; flip angle = 90°). Encoding session consisted 1065 ± 4.2 scans and retest session 950 ± 7.6 scans. The three initial scans were discarded to allow for magnetic saturation effects. Head movements were minimized using a vacuum cushion. A structural T1-weigthed three-dimensional MP-RAGE sequence (repetition time = 1960 msec, echo time = 4.43 msec, inversion time = 1100 msec, field of view = 230 × 173 cm^2, matrix size = 256 × 256 × 176, voxel size = 0.9 × 0.9 × 0.9 mm) was also acquired in all participants at the end of the retest session. Stimuli were displayed on a screen positioned at the rear of the scanner, which the subject could comfortably see through a mirror mounted on the standard head coil.

Functional volumes were preprocessed and analyzed using Statistical Parametric Mapping 2 (http://www.fil.ion.ucl.ac.uk/spm/software/spm2/; Wellcome Department of Imaging Neuroscience, London, UK) implemented in MATLAB (MathWorks Inc., Sherbom, MA). They were realigned using iterative rigid body transformations that minimize the residual sum of square between the first and the subsequent images. They were corrected for head motion, spatially normalized to an EPI template conforming to the Montreal Neurological Institute space, and spatially smoothed with a Gaussian Kernel of 8-mm FWHM.

The analysis of fMRI data, on the basis of a mixed effects model, was conducted in two serial steps, accounting for fixed and random effects, respectively. For each subject, changes in brain regional responses were estimated using a general linear model.

During the retest session, 12 trial types were modeled: studied words correctly remembered ("old" words, O-R), studied words identified as known (O-K), studied words identified as new (O-N), critical theme words (lures) correctly identified as new (L-N), lures identified as remembered (L-R), lures identified as known (L-K), distractor words related to presented words correctly identified as new [D(O)-N], distractor words related to presented words identified as remembered [D(O)-R], distractor words related to presented words identified as known [D(O)-K], distractor words related to lures correctly identified as new [D(L)-N], distractor words related to lures identified as remembered [D(L)-R], and distractor words related to lures identified as known [D(L)-K]. For each trial type, a given item was modeled as a delta function representing its onset. The ensuing vector was convolved with the canonical hemodynamic response function and used as a regressor in the individual design matrix. Movement parameters derived from realignment of the functional volumes and constant vector were included in the matrix design as a variable of no interest. High-pass filtering was implemented using a cut-off period of 128 sec to remove low frequency drifts from the time series. Serial correlations in fMRI signal were estimated using an autoregressive (Order 1) plus

white noise model and a restricted maximum likelihood (ReML) algorithm. Linear contrasts tested for the differential effect of recollection versus familiarity responses for studied words (O), lure (L), and distractor related. The resulting set of voxel values generated statistical parametric maps [(SPM(T)]. The individual summary statistic images resulting from these different contrasts were then further spatially smoothed (6-mm FWHM Gaussian kernel) and entered in a second-level analysis, corresponding to a random effects model. This second step accounted for intersubject variance and consisted of two-sample t tests testing the differences between groups and one-sample t tests testing for the effect of interest separately in each group. The resulting set of voxel values for each contrast constituted a map of the t statistics [SPM(T)], thresholded at $p < .001$ (uncorrected for multiple comparisons). Exclusive masks were created with SPM maps thresholded at $p < .05$. Statistical inferences were performed at a threshold of $p < .05$ after correction for multiple comparisons over either the entire brain volume or the small spherical volumes (10 mm radius). Small volume corrections (SVCs) were conducted around a priori locations of activation in structures of interest, reported by published works (see Tables 2 and 3).

To analyze the encoding session, we first categorized for each subject the lists listened at the encoding session in lists that ultimately would generate a lure, either through recollection (List-L-R) or through familiarity (List-L-K), and the lists that did not produce any lure (List-L-N). The analysis of fMRI data was conducted in two serial steps, taking into account the intraindividual and the interindividual variance, respectively. For each subject, changes in brain regional responses were estimated by a general linear model including the three trial types: List-L-R, List-L-K, and List-L-N. Linear contrasts estimated the main effect of lure categorization. The resulting set of voxel values constituted a map of t statistics [SPM(T)]. The summary statistical images were fed into the second level analysis that consisted of one-sample t tests testing for the effect of interest. Statistical inferences were conducted as for the retrieval session.

RESULTS

Sleep Parameters

No significant difference on mean subjective sleep duration was observed between SD and S groups on the night preceding the encoding, $F(1, 36) = 0.64$, $p = .6$, and the night preceding the retest session, $F(1, 36) = 1.47$, $p = .3$. Mean subjective sleep duration was longer for the SD than for the S group for the second postencoding night, $F(1, 36) = 14.83$, $p < .0001$, consistent with the expected sleep rebound after deprivation.

Subjective sleep quality was determined with a 10-point scale. Mean subjective sleep quality was not significantly different between groups on the night preceding the

Table 1. Behavioral Data

Memory Performance (%)	"Remember"					"Know"					"New"				
	O	L	D(S)	D(L)	Mean	O	L	D(S)	D(L)	Mean	O	L	D(S)	D(L)	Mean
Sleep group (S)	33.8 ± 16.7	33.9 ± 18.7	6.8 ± 11	7.8 ± 13.5	20.56 ± 14.96	28.9 ± 10.3	35.2 ± 17.6	17.1 ± 12.5	20.5 ± 13.3	30.89 ± 12.86	37.3 ± 15.1	30.9 ± 15.4	76 ± 17.3	71.7 ± 18	53.97 ± 16.61
Sleep-deprived group (SD)	20.5 ± 12.9*	22.7 ± 15.2	1.6 ± 2.1	1.7 ± 2.7	11.64 ± 8.21	39.8 ± 9.5**	41.7 ± 17	19.5 ± 9.8	22.6 ± 15.1	25.46 ± 13.42	39.7 ± 14.2	35.4 ± 20	78.8 ± 11.1	75.7 ± 15.8	57.6 ± 14.73
Mean	27.13 ± 6.18	28.30 ± 17.69	4.77 ± 10.06	4.21 ± 8.23		34.38 ± 11.2	38.45 ± 17.36	18.34 ± 11.15	21.53 ± 14.07		38.5 ± 14.3	33.15 ± 17.2	77.4 ± 15.3	73.7 ± 12.23	

O = presented words; L = critical theme words (lure); D(S) = distractor words related to presented words; D(L) = distractor words related to critical lure.

*Significantly different from the S group ($p < .05$).

**Significantly different from the S group ($p < .005$).

Table 2. Brain Responses Recorded during Retrieval

Region	x	y	z	Z Score	p_{svc}	Reference
OR > OK in S (Exclusive Masking with SD)						
Ventral medial pFC	−2	40	−14	3.59	.014	Takashima et al. (2006)
Superior frontal sulcus	−28	28	38	4.03	.003	Eldridge, Knowlton, Furmanski, Bookheimer, and Engel (2000)
Retrosplenial cortex	10	−48	22	4.73	.002	Henson, Hornberger, and Rugg (2005)
Angular gyrus	50	−66	22	4.18	.002	Henson et al. (2005)
Temporal pole	−46	2	−34	3.17	.042	Henson et al. (2005)
Posterior hippocampus	−30	−16	−16	4.00	.004	Eldridge et al. (2000)
Parahippocampal gyrus	14	−36	−8	3.60	.013	Eldridge et al. (2000)
OR > OK in SD (Exclusive Masking with S)						
Polar medial pFC	2	54	−4	4.85	<.001	Henson et al. (2005)
Middle frontal gyrus	−38	4	54	3.31	.034	Konishi, Wheeler, Donaldson, and Buckner (2000)
Inferior frontal gyrus	−44	22	−18	4.43	.001	Henson et al. (2005)
	50	20	−18	3.44	.024	Henson et al. (2005)
Posterior intraparietal sulcus	−32	−68	50	4.15	.003	Konishi et al. (2000)
	32	−70	52	4.53	.001	Konishi et al. (2000)
Supramarginal gyrus	−56	−58	24	3.58	.016	Henson et al. (2005)
	48	−54	22	3.51	.020	Henson et al. (2005)
Posterior cingulate cortex	−6	44	38	3.84	.007	Henson et al. (2005)
Precuneus	−4	−72	52	4.44	.001	Konishi et al. (2000)
Anterior STS	−52	−36	−8	4.94	<.001	Henson et al. (2005)
	60	−34	−8	3.98	.005	Henson et al. (2005)
Cuneus	14	−94	16	4.82	<.001	Henson et al. (2005)
Ventral striatum	−8	12	−2	4.44	.001	Eldridge et al. (2000)
	8	12	−2	4.38	.001	Eldridge et al. (2000)
LR > LK in S (Exclusive Masking with SD)						
Retrosplenial cortex	14	−60	20	3.87	.007	Eldridge et al. (2000)
Hippocampus	−24	−26	−18	3.77	.009	Cabeza et al. (2001)
LR > LK in SD (Exclusive Masking with S)						
Middle frontal gyrus	−40	10	58	3.98	.005	Henson et al. (2005)
Inferior frontal gyrus	−36	28	0	4.85	<.001	Henson et al. (2005)
	40	30	−8	4.68	<.001	Henson et al. (2005)
Posterior intraparietal sulcus	−32	−70	48	3.43	.026	Henson et al. (2005)
	36	−62	42	3.38	.029	Henson et al. (2005)
Anterior STS	56	−32	−16	4.33	.002	Henson et al. (2005)

Table 2. (continued)

Region	x	y	z	Z Score	p_{svc}	Reference
OR > LR in S (Exclusive Masking with SD)						
Inferior parietal lobule	−44	−38	32	3.29	.038	Eldridge et al. (2000)
Fusiform gyrus	26	−58	−10	3.37	.031	Eldridge et al. (2000)
Parahippocampal gyrus	−28	−34	−16	3.63	.015	Eldridge et al. (2000)

x,y,z = coordinates in the Montreal Neurological Institute space; p_{SVC} = significance after correction for multiple comparisons on small VOI reported in the literature (specified in the last column).

the encoding, $F(1, 36) = 0.008$, $p = .92$, and the night preceding retest session, $F(1, 36) = 0.12$, $p = .8$. Mean subjective sleep quality was equivalent between groups on the second postencoding night, $F(1, 36) = 2.46$, $p = .38$.

The night preceding the encoding session and the three nights after this encoding session were recorded with actigraphy. Significant difference on actigraphic data was observed between groups, $F(1, 34) = 142.32$, $p < .001$, and between nights, $F(3, 102) = 171.9$, $p < .001$. The interaction group by night was also significant, $F(3, 102) = 148.5$, $p < .001$. The activity of SD and S groups did not differ during the night before encoding session, $F(1, 34) = 0.26$, $p = .82$. During the first night after encoding session, as expected, the activity was larger in the SD than that in the S group, $F(1, 34) = 127.2$, $p < .001$. A rebound of deep sleep after sleep deprivation is suspected by a lower activity in SD than that in S participants during the second night after encoding session, $F(1, 34) = 7,43$, $p = .042$. This effect was no longer present on the third night after encoding session, which preceded the retest session, $F(1, 34) = 2.14$, $p = .38$, suggesting that two nights were sufficient to recover from sleep deprivation.

Alertness

Alertness was objectively measured right before fMRI sessions. RTs in a psychomotor vigilance task (PVT) did not differ between groups in the two sessions: encoding session, S = 277 ± 6.3, SD = 281 ± 5.8, $F(1, 34) = 1.43$, $p =$ .23; retest session, S = 278 ± 5.2, SD = 280 ± 4.7, $F(1, 34) = 0.99$, $p = .32$.

Behavioral Results

The behavioral results are detailed in Table 1 and Figure 2.

Overall Recognition Performance (R + K Responses)

To examine the overall recognition performance (R + K responses), we performed a 2 (Group: S vs. SD) × 4 (Items: old O vs. Lures L vs. distractors matched to studied Item DS or to critical lures DL) ANOVA with repeated measures on the last factor on the rates of "old" responses assigned to the different kinds of items. This analysis revealed no significant effect of Group, $F(1, 34) = 0.67$, $p = .41$, showing that SD participants (46.02 ± 14.14%) did not recognized less items than S group (42.53 ± 15.22%), consistent with a previous report conflating R and K responses (Diekelmann et al., 2008). Only the main effect of Item was significant, $F(2, 102) = 183,79$, $p < .0001$. Planned comparisons showed that lures (66.75 ± 17.68%) were recognized (R + K responses) more often than studied items (61.5 ± 14.46%). Both of these responses were recognized more often than both kinds of distractors. However, distractors matched to lures (26.3 ± 16.83%) were recognized more often than distractors matched to studied items (22.55 ± 14.39%), which is also in agreement with previous literature (Gallo, 2006). This means that participants rejected correctly more often

Table 3. Brain Responses Recorded during Encoding and Associated with Subsequent Accurate Recollection (OR), Relative to Illusory Recollection (LR)

Region	x	y	z	Z Score	p_{svc}	Reference
Precentral cortex	52	−2	54	3.90	.004	Ranganath et al. (2004)
Occipito-temporal sulcus	−64	−50	−14	3.90	.004	Aminoff, Schacter, and Bar (2008)
Hippocampus	34	−34	−10	2.57	.012	Uncapher and Rugg (2008)
Parahippocampal gyrus	−30	−42	−8	3.77	.006	Ranganath et al. (2004)
Thalamus	−12	−4	6	3.72	.008	Ranganath et al. (2004)

x,y,z = coordinates in the Montreal Neurological Institute space; p_{SVC} = significance after correction for multiple comparisons on small VOI reported in the literature (specified in the last column).
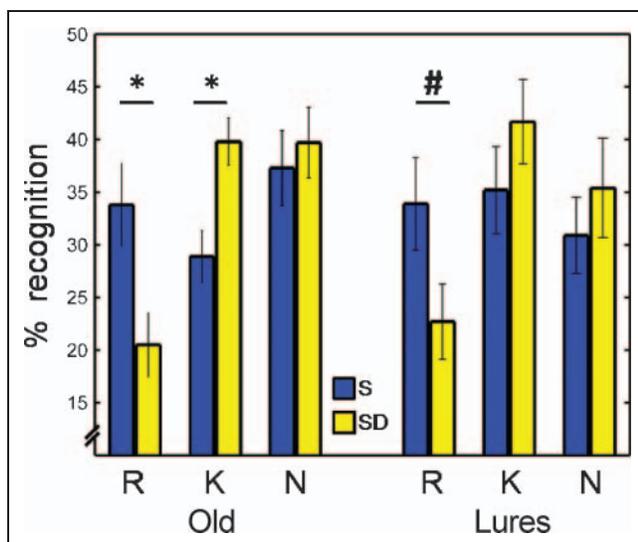
Figure 2. Percent recognition in terms of Remember (R), Know (K), and New (N) responses. Left and right panels: accurate and illusory recognition, respectively. Blue and Yellow bars: S and SD group, respectively. *$p < .05$; #$p = .058$.

DS (73.70 ± 16.83) and DL (74.44 ± 14.4) than they falsely rejected studied (38.5 ± 14.5) and correctly rejected lures (33.18 ± 17.7). The Group × Item interaction was not found significant, $F(3, 102) = 0.094$, $p = .96$.

Recollection versus Familiarity

The ANOVA performed on the proportion of recollection responses (i.e., "Remember" judgments assigned to recognized responses) showed a significant main effect of Group, $F(1, 34) = 6.99$, $p = .012$, with S participants ($20.56 \pm 14.96\%$) correctly assigning more remember responses than SD participants ($11.64 \pm 8.21\%$). The main effect of Item was also significant, $F(3, 102) = 74.70$, $p < .0001$. Planned comparisons showed that the rates of recollection responses were similar between studied items ($27.13 \pm 16.18\%$) and lures ($28.30 \pm 17.69\%$) and higher than the recollection responses assigned to both kind of distractors. The rates of recollection assigned to DS ($4.77 \pm 10.06\%$) and DL ($4.21 \pm 8.23\%$) were similar.

Importantly, there was no significant Group × Item interaction, $F(3, 102) = 1.58$, $p = .20$. Exploratory planned comparisons showed, however, that S participants assigned more recollection judgments than SD participants to studied items ($33.8 \pm 16.7\%$ vs. $20.5 \pm 12.9\%$, $p = .011$), lures (33.9 ± 18.7 vs. 22.7 ± 15.2, $p = .058$), DL ($p = .056$), and DS ($p = .069$). Quantitatively, the enhancement of memory retention after sleep, relative to sleep deprivation, was similar for false and true recollection (i.e., a gain in recollection of about 12% was observed for both trial types in S relative to SD) and was also observed for distractors.

Finally, the analysis performed on the proportion of "Familiar" judgments showed that overall S participants did not produce more familiar judgments ($25.46 \pm 13.42\%$) than SD participants ($30.89 \pm 12.86\%$), $F(1, 34) = 1.62$, $p = .21$. The main effect of item was significant, $F(3, 102) = 34.85$, $p < .0001$. Planned comparisons showed that overall lures ($38.45 \pm 17.36\%$) received more "Familiar" judgments than studied items ($34.38 \pm 11.2\%$). These proportions were higher than that assigned to DL ($21.53 \pm 14.07\%$), in turn more important than the judgments assigned to DS ($18.34 \pm 11.15\%$). Although the Group × Item interaction was not significant, $F(3, 102) = 1,55$, $p = .20$, planned comparisons showed that S participants assigned familiar judgments to lures, DS, and DL in similar way than that of SD participants. However, SD participants were more likely to be assigned to familiar judgments than to studied items ($39.8 \pm 9.5\%$) than S participants ($28.9 \pm 10.3\%$, $p < .005$).

In summary, sleep deprivation did not affect the overall proportion of recognition. However, SD participants tended to assign less recollection responses to studied items, lures, and distractors while they were more likely to assign familiar judgments to studied items.

Functional MRI Results

Brain responses associated with accurate recollection (R relative to K responses for "old" words, OR > OK) did not significantly differ between groups, likely because of a large response variance in the SD group. However, the responses elicited by accurate recollection (OR > OK) were differently distributed between groups. In the S group but not in the SD group (exclusive masking), recollection was associated with significant responses in the left posterior hippocampus, the right parahippocampal gyrus, the left ventral medial prefrontal, and the right retrosplenial cortices (Table 2, Figure 3, green). In contrast, participants in the SD group (but not in the S group, exclusive masking) recruited a large set of associative frontal, parietal, temporal, and occipital areas during accurate recollection (Table 2, Figure 4A).

Similarly, false recollections (R relative to K responses for critical lures, LR > LK) observed at behavioral level did not significantly differ between groups. However, they were associated with increased cerebral activity in the left posterior hippocampus and right retrosplenial cortex, only if sleep was allowed on the first postencoding night (exclusive masking by SD group; Table 2, Figure 3, red). In the S group, the hippocampal and the retrosplenial responses associated with accurate and false recollections spatially overlapped, suggesting the contribution of a common network for the retrieval of true and false memories (Figure 3A and C). However, in the S group, accurate recollection differed from illusory recollection (OR > LR) by significantly larger responses in the left parahippocampal gyrus, left inferior parietal lobule, and right fusiform gyrus (Table 2, Figure 5).

In contrast, in the SD group (and not in the S group, exclusive masking), recollection of lures was associated with responses in a distributed set of frontal, parietal, temporal, and occipital areas (Figure 4B).

Although the response patterns elicited by recollection (i.e., episodic memory retrieval) differed between S and SD groups and suggested a different off-line processing during the postencoding night, the absence of significant between-group differences suggested that the novel associations giving rise to illusory recollections did not primarily arise during sleep. Indeed, we gained objective evidence that the engrams created during encoding already differ
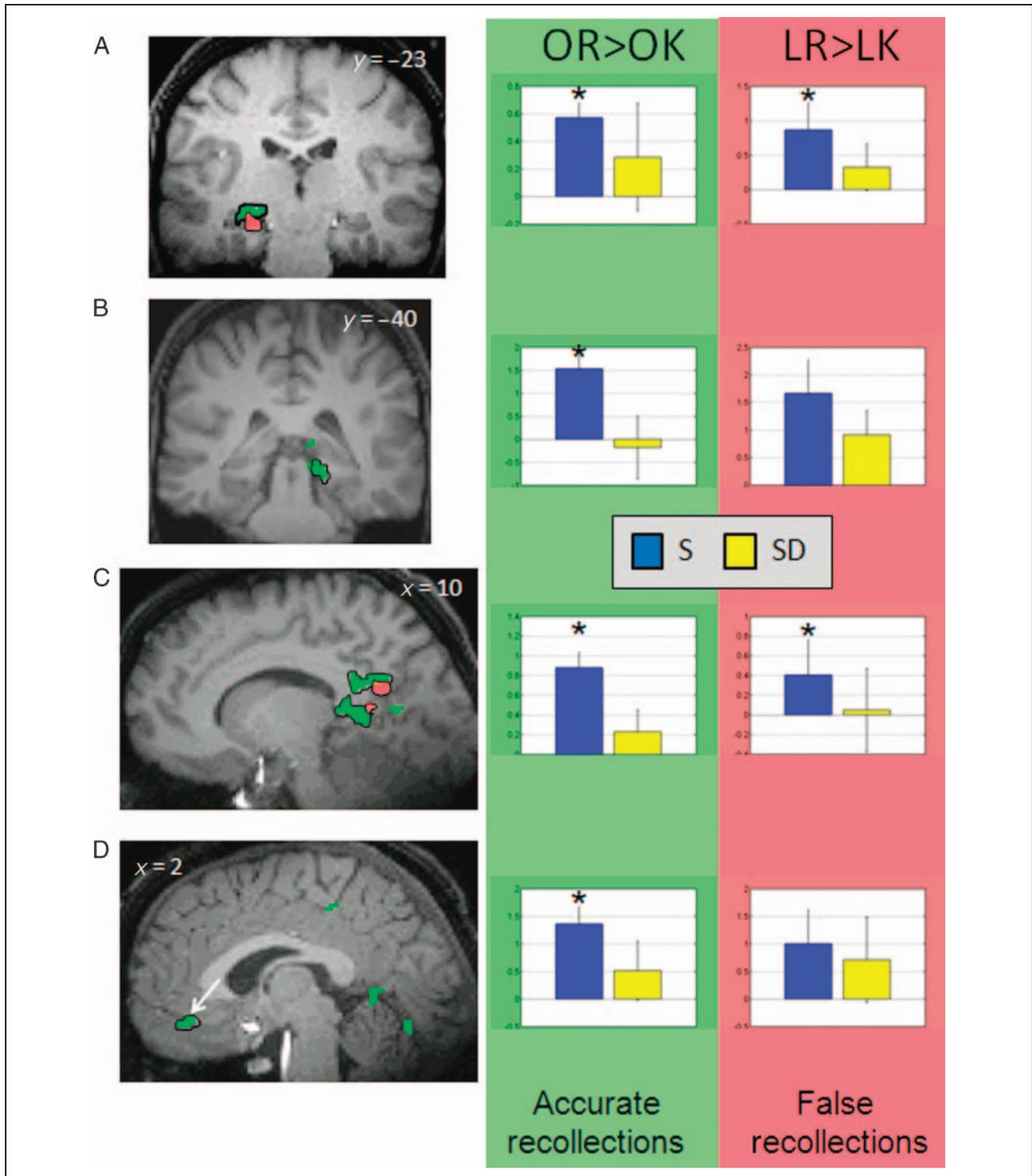

Figure 3. Brain areas associated with larger responses during recollection than familiarity-based recognition, for accurate (green) and illusory (red) memories, in S and not in SD. (A) Left anterior hippocampus. (B) Right parahippocampal gyrus. (C) Retrosplenial cortex. (D) Ventromedial pFC. Results are displayed at $p_{uncorrected} < .001$, superimposed on an individual structural MR scan normalized to the Montreal Neurological Institute space. Activity estimates (arbitrary units) are displayed in blue and yellow for S and SD group, respectively. *$p_{SVC} < .05$.
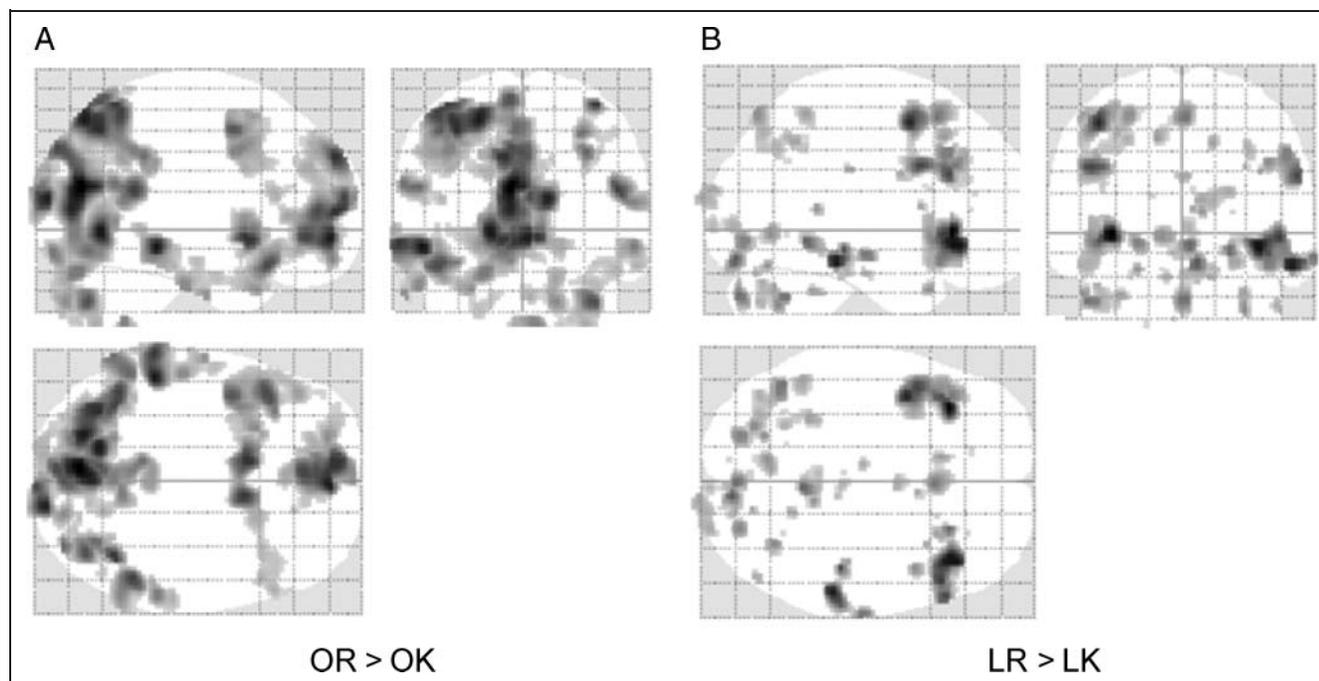
Figure 4. Brain responses associated with recollection in SD group and not in S group, displayed in transparent brain in the three axes (threshold $p < .001$). (A) OR > OK. (B) LR > LK.

between the lists that will and those that will not subsequently lead to false recollection, irrespective of whether the participants are subsequently sleep deprived. Across all participants (S and SD), the lists that eventually did not produce false recollection of lures were characterized during encoding by a larger activity in the posterior hippocampus compared with the lists that were associated with a later recollection of the lure (Table 3, Figure 6). This is an important result because it implies that off-line processes potentially taking place during sleep were modifying qualitatively different memories depending on the way they were encoded in the first place.

DISCUSSION

One objective of this study was to assess the effect of sleep and lack of sleep during the postencoding night on the neural correlates of subsequent accurate and false memories, using DRM paradigm and fMRI. Our results show that after both sleep and sleep deprivation, accurate and illusory recollections were enhanced and were associated with significant responses in the hippocampus and retrosplenial cortex. After sleep, the accurate recollection differed from false recollection by the recruitment of parahippocampal gyrus. Nevertheless, direct between-group comparison of fMRI data did not reveal any significant difference between sleep and sleep deprivation conditions, suggesting that sleep during the first postencoding night does not prominently influence the off-line processing of false memories. In contrast, we show that the early recruitment of hippocampus during encoding strongly conditions the subsequent quality of recollec-

tion 3 days later. Although sleep to some extent modifies brain responses associated with accurate and false recollections, the eventual behavioral performance at retrieval seems more dependent on the encoding strategy than to a differential effect of sleep on memories subsequently accurately or falsely recollected.

Sleep Enhances Accurate and Illusory Recollections, Relative to Sleep Deprivation

Sleep, relative to sleep deprivation, did not significantly modify overall behavioral recognition performance (R + K responses). However, recollection, that is, the process of correctly recognizing an item on the basis of the retrieval of specific contextual details (R responses) rather than by familiarity (K responses), was specifically enhanced after sleep as compared with sleep deprivation. These results confirm earlier reports showing a beneficial effect of sleep on contextually rich episodic memories (Gais et al., 2007; Gais, Lucas, & Born, 2006) and support the theory that sleep promotes the consolidation of veridical declarative memories.

We also observed an increased proportion of false recollections (R responses to lures) in the sleep group, relative to the sleep deprivation condition, although the difference just fell short of significance ($p = .058$). These results are in line with a recent study that showed an increase in recall of critical lures over studied words after sleep compared with equivalent periods of wakefulness (Payne et al., 2009). Collectively, the results suggest a beneficial effect of sleep on the production of false memories. However, contrary to that study, we do not confirm

that sleep has a bigger impact on false than accurate memories. The results do not show a selective enhancement of false recollections, relative to other trial types after sleep, as compared with sleep deprivation (the Group × Item interaction was not significant). In particular, the enhancement of memory retention across sleep conditions was comparable for accurate and illusory recollections (~12%). This discrepancy can result from differences in retrieval processes between studies. Although we tested recognition using a remember/know procedure, Payne et al. (2009)

resorted to free recall, which might be differently sensitive to the production of false memories.

Our results contrast with a recent study that did not report any significant enhancement of false recognition after sleep, relative to wakefulness (Diekelmann et al., 2008). In particular, similarly to the present study, participants in their Group 3 were either allowed to sleep or were sleep deprived during the postencoding night and were tested after one recovery night. They report a larger proportion of false recollections after sleep deprivation
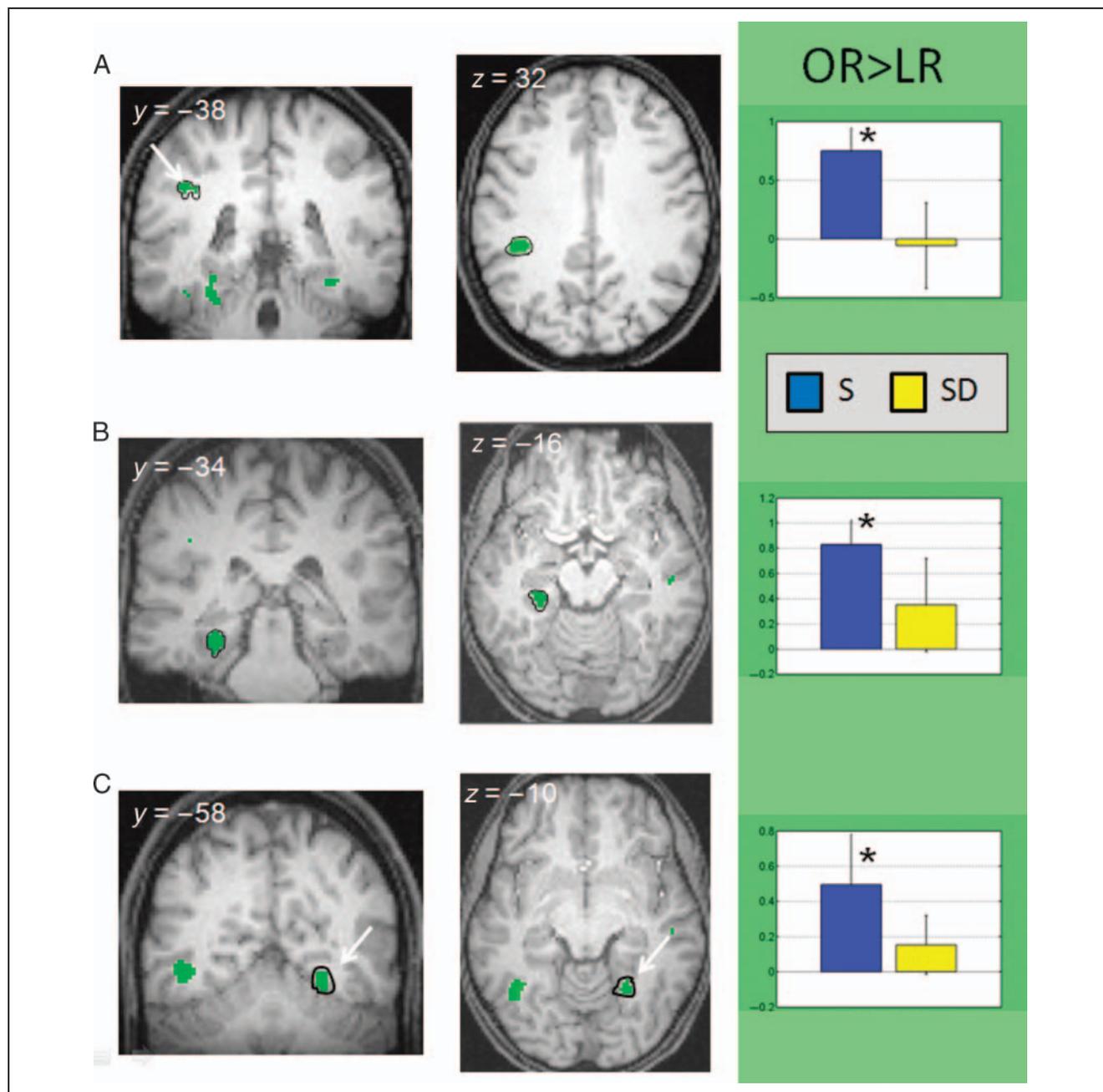
Figure 5. Brain areas associated with larger responses during accurate than illusory recollection, in S and not in SD. (A) Left inferior parietal lobule. (B) Left parahippocampal gyrus. (C) Right fusiform gyrus. Results are displayed at $p_{uncorrected} < .001$, superimposed on an individual structural MR scan normalized to the Montreal Neurological Institute space. Activity estimates (arbitrary units) are displayed in blue and yellow for S and SD group, respectively. $*p_{SVC} < .05$.
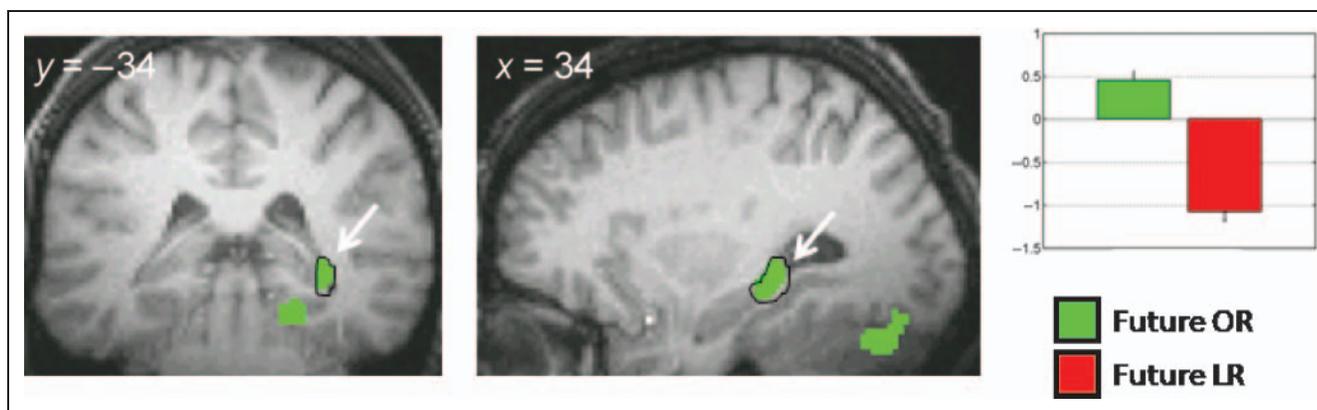
Figure 6. Larger responses for lists that will subsequently lead to accurate relative to illusory recollection in the right posterior hippocampus. Results are displayed at $p_{\text{uncorrected}} < .001$, superimposed on an individual structural MR scan normalized to the Montreal Neurological Institute space. Right panel: Activity estimates (arbitrary units) are displayed in green and red for accurate and illusory recollection, respectively.

(43%) than after sleep (39%), a nonsignificant difference. In contrast to our own and previous findings, accurate recognition rates were also not modified by sleep condition (Diekelmann et al., 2008). Finally, they also report a larger proportion of false alarms (14–19% in the study of Diekelmann et al., 2008, 1–7% in our study), which suggests that their participants adopted a more liberal retrieval strategy than ours. These discrepancies are potentially explained by various experimental factors: the number of lists (18 lists instead of 32 lists, in the study of Diekelmann et al., 2008, and our study, respectively), the time limitation for retrieval (no time limit instead of 10 sec), the procedure of sleep deprivation (stronger control on light level, activity, food intake in our study), and the conditions inherent to fMRI acquisitions during encoding and retrieval. All of these factors can eventually alter the subtle effects elicited by the DRM paradigm.

Nevertheless, our results are consistent with the study of Diekelmann et al. (2008) in that the differential effect of sleep and sleep deprivation on false recollection rates is statistically weak. Taken together, it seems fair to say that the behavioral studies available so far show at best only a moderate enhancement of subsequent false recollection by sleep, relative to sleep deprivation.

Sleep Moderately Influences the Neural Correlates of Subsequent False and Illusory Recollection Elicited by the DRM Paradigm

Functional MRI data show definite but moderate changes in the neural correlates of accurate and false recollection (R > K) after sleep, relative to sleep deprivation. On the one hand, no significant difference is detected when comparing brain responses associated with (accurate or false) recollection after sleep relative to sleep deprivation. This negative result can find various explanations. First, a large variability in brain response is observed in sleep-deprived participants (see several examples on Figure 3), which considerably weakens the sensitivity of the statistical analysis and might suggest a lack of power of

the experiment. However, other experiments conducted in our laboratory, assessing sleep-dependent memory consolidation on the basis of the same sleep deprivation protocol and similar sample sizes, did show significant changes in neural correlates at retrieval between groups (Sterpenich et al., 2007, 2009; Gais et al., 2007; Orban et al., 2006). Second, the lack of effect might be related to the DRM paradigm itself and its adaptation to fMRI settings. The difficulty of memorizing a large number of strongly semantically related words (32 lists of 15 words, i.e., 480 words instead 8 lists of 15 words in most behavioral studies) could result in a lesser activation of the associated themes in our learning phase and subsequent decayed traces at recognition. However, the overall recognition rates observed in the present study (around 60%) are not dramatically lower than that in our previous experiments (see for instance Sterpenich et al., 2007) or in experiments assessing effects of delay comparable to what we used in the DRM paradigm (e.g., Seamon et al., 2002; Thapar & McDermott, 2001). Third, a residual influence of sleep deprivation on retrieval processes might be considered because false recollections have been associated with different retrieval strategies in sleep-deprived volunteers (Diekelmann et al., 2008). However, in our case, participants were allowed to sleep at least two complete nights before retrieval, which makes unlikely any difference in alertness between groups that might arise from earlier sleep deprivation. Objective measures of alertness sampled in all participants before fMRI sessions using PVT confirmed that alertness was comparable between groups.

On the other hand, the distribution of brain responses associated with recollection differed between groups, as revealed by exclusive masking. In the sleep group, significant responses in the left posterior hippocampus and in the retrosplenial cortex were associated with both accurate and false recollections (R > K). These two regions are well known to be recruited by accurate recollection (Yonelinas, Otten, Shaw, & Rugg, 2005; Ranganath et al., 2004). A significant hippocampal response has also been previously associated with the retrieval of false memories,

and it was suggested that it was involved in the recovery of semantic rather than sensory information (Cabeza, Rao, Wagner, Mayer, & Schacter, 2001). In contrast, although the precuneus (Cabeza et al., 2001) and the midcingulate gyrus (Kim & Cabeza, 2007) have already been associated with retrieval of false memories, it is, to the best of our knowledge, the first time that retrosplenial responses are observed during illusory recollection. This result is important because retrosplenial cortex has been proposed to process items on a general, prototypical level, analyzing long-term associations of the current stimulus (i.e., the memory gist) rather than its perceptual details (Bar & Aminoff, 2003). Beyond these commonalities, there were also significant differences between accurate and false recollections in the sleep group: Responses were larger for the former than for the latter in left parahippocampal gyrus, left inferior parietal lobule, and right fusiform gyrus. The selective involvement of these posterior areas during accurate recollection has been attributed to the recovery (parahippocampal gyrus; Cabeza et al., 2001) and accumulation (parietal cortex; Wagner, Shannon, Kahn, & Buckner, 2005) of detailed perceptual information and their association with contextual information (visual cortices; Bar & Aminoff, 2003). Their larger response to accurate than illusory recollection suggests a better access in the former case to perceptual information before memory decision.

The detection of these responses selectively in the group of participants allowed to sleep during the postencoding night supports the hypothesis that sleep promotes the systems-level reorganization of recent memories in hippocampal–neocortical networks in keeping with previous work on veridical declarative memory retrieval (Gais et al., 2007; Sterpenich et al., 2007; Takashima et al., 2006). In contrast, in the sleep deprivation group, the response pattern to both accurate and illusory recognition was characterized by the recruitment of distributed cortical areas, suggesting that sleep-deprived participants developed more effortful and controlled strategies than the sleep group to retrieve information (Chein & Schneider, 2005).

Early Recruitment of Hippocampus during Encoding Predicts Subsequent False Memories, Irrespective of Sleep or Lack of Sleep during the Postencoding Night

Although the results detailed above suggest that sleep reorganized both accurate and false memories, this effect seems moderate and does not suggest that the formation of novel associations leading to false memories arise primarily during sleep. For this reason and because we previously showed using the same material that participants often conjure up the critical lures during encoding (Dehon & Brédart, 2004), we tested the hypothesis that brain responses recorded during encoding would differ between the lists that would subsequently produce a false recol-

lection and those who would not. These responses taking place before the experimental manipulation of sleep should be observed across the whole population. Indeed, irrespective of the subject group (S or SD), the lists that eventually did not produce false recollection of lures were characterized during encoding by a larger activity in the hippocampus compared with lists that were associated with a later recollection of the lure. It is established that the posterior hippocampus supports deep associative encoding that selectively contributes to later accurate recollection (Ranganath et al., 2004). In particular, the activity in left posterior hippocampus during encoding has been associated with high confidence in accurate recollection (hits) rather than false recognitions (Kim & Cabeza, 2007; Okado & Stark, 2005). In the absence of substantial recruitment of the posterior hippocampus during encoding, the high similarity of the associates composing the lists and the critical theme word would simply render more difficult the distinction between accurate and illusory memories during retrieval (Chalfonte & Johnson, 1996).

Conclusion

Sleep promotes both accurate and illusory recollections, which are both associated with conspicuous hippocampal and retrosplenial responses. The absence of significant difference between experimental groups does not suggest that sleep is a prominent factor in determining the occurrence of subsequent false recollections. In contrast, response patterns during encoding, especially in the hippocampus, seem to foreshadow the production of accurate recollections rather than illusory memories. The proportion of lures evoked at retrieval seems to depend primarily on the quality of encoding because false recollections essentially relate to the lists encoded in a superficial manner. Our data do not support the view of a specific effect of sleep in extracting and consolidating the gist of memories. In contrast, they support a general favorable effect of sleep on declarative/episodic memories, through a reinforcement of associations of various kinds and strength involving the hippocampus and the neocortical areas.

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