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The impact of overnight consolidation upon memory for emotional and neutral encoding contexts

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ABSTRACT

Sleep plays a role in the consolidation of declarative memories. Although this influence has attracted much attention at the level of behavioural performance, few reports have searched for neural correlates. Here, we studied the impact of sleep upon memory for the context in which stimuli were learned at both behavioural and neural levels. Participants retrieved the association between a presented foreground object and its encoding context following a 12-h retention interval including either wake only or wake plus a night of sleep. Since sleep has been shown to selectively enhance some forms of emotional memory, we examined both neutral and emotionally valenced contexts. Behaviourally, less forgetting was observed across retention intervals containing sleep than retention intervals containing only wakefulness, and this benefit was accompanied by stronger responses in hippocampus and superior parietal cortex. This sleep-related reduction in forgetting did not differ between neutral and negative contexts, but there was a clear interaction between sleep and context valence at the functional level, with left amygdala, right parahippocampus, and other components of the episodic memory system all responding more strongly during correct memory for emotional contexts post-sleep. Connectivity between right parahippocampus and bilateral amygdala/periamygdala was also enhanced during correct post-sleep attribution of emotional contexts. Because there was no interaction between sleep and valence in terms of context memory performance these functional results may be associated with memory for details about the emotional encoding context rather than for the link between that context and the foreground object. Overall, our data show that while context memory decays less across sleep than across an equivalent period of wake, the sleep-related protection of such associations is not influenced by context emotionality in the same way as direct recollection of emotional information.

1. Introduction

Consolidation is the gradual reorganisation and stabilisation of labile, newly encoded memories (McGaugh, 2000). Both lesion work and neuroimaging suggest that consolidation involves alterations in the way memories are represented in the brain such that they cease to depend upon the hippocampus and become increasingly integrated with existing neocortical traces (Eichenbaum, 2000; Frankland & Bontempi, 2005).

A growing literature supports a role for sleep, particularly slow wave sleep (SWS), in declarative memory consolidation (Benedict, Scheller, Rose-John, Born, & Marshall, 2009; Gais & Born, 2004; Lau, Tucker, & Fishbein, 2010; Plihal and Born, 1997; Rasch, Buchel, Gais, & Born, 2007; Takashima et al., 2006), see (Born, 2010; Diekelmann & Born, 2010; Walker, 2009) for reviews, but see also (Vertes, 2004). This includes work showing reduced episodic memory decay across sleep as compared to wakefulness (Takashima et al., 2006), enhanced episodic memory after sleep (Plihal & Born, 1997), and enhanced episodic memory after artificial stimulation of slow-waves (Marshall, Helgadottir, Molle, & Born, 2006). Additionally, work in both rats (Hoffman & McNaughton, 2002; Nadasdy, Hirase, Czurko, Csicsvari, & Buzsaki, 1999; Wilson & McNaughton, 1994) and humans (Maquet et al., 2000; Peigneux et al., 2004; Rasch et al., 2007) shows that the neural ensembles associated with learning reactivate spontaneously during sleep, and that such reactiva-

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tion can predict subsequent performance improvements (Peigneux et al., 2004). Few studies have extended these observations to examine the brain correlates through which overnight sleep influences the consolidation of declarative memories in humans, but see (Takashima et al., 2006) for work on daytime napping, and (Gais et al., 2007) for a study using sleep deprivation.

A number of reports (Hu, Stylos-Allan, & Walker, 2006; Nishida, Pearsall, Buckner, & Walker, 2009; Payne, Stickgold, Swanberg, & Kensinger, 2008; Payne & Kensinger, 2011; Sterpenich et al., 2007, 2009; Wagner, Degirmenci, Drosopoulos, Perras, & Born, 2005; Wagner, Hallschmid, Rasch, & Born, 2006) suggest that sleep plays a selective role in the consolidation of emotional memories. While neutral memories are gradually forgotten over time (Frankland & Bontempi, 2005; McGaugh, 2000) such decay is less apparent in emotional memories (LaBar & Cabeza, 2006) for a review. Retention of emotional memories across sleep has been associated both with reduced decay (Wagner et al., 2005, 2006) and with facilitated enhancement (Hu et al., 2006; Nishida et al., 2009; Payne & Kensinger, 2011; Payne et al., 2008) compared to neutral memories or retention across equivalent periods of wake. To date, this work is largely behavioural, but there is increasing interest in the effects of sleep and sleep deprivation on the neural correlates of memory for emotional material (Payne & Kensinger, 2011; Sterpenich et al., 2007, 2009).

In the current report, we set out to extend this literature by examining the impact of sleep upon memory for the context in which presented images were first encountered. We studied both neutral and negative contexts, and used functional magnetic resonance imaging (fMRI) to examine the impact of retention across a 12-h period containing either wakefulness alone or wakefulness plus a night of sleep. Because retrieval-related responses in the amygdala and hippocampus, as well as connectivity between these, are modulated by instructions at test, we used a paradigm which elegantly manipulates this factor (Smith, Henson, Rugg, & Dolan, 2005; Smith, Stephan, Rugg, & Dolan, 2006). Thus, contextual stimuli were presented only at encoding, where they were paired with neutral objects that were later presented as retrieval cues. Participants indicated whether these cues were originally paired with an emotional or neutral image (explicit emotional memory task) or an image containing people or no people (implicit emotional memory task). This paradigm provides two important advantages in the study of emotional memory. First, because only neutral information is presented at test, retrieval-related responses in the emotional memory system cannot be due to the mere processing of externally presented emotional stimuli, and are more likely associated with emotional memory. Second, unlike more traditional recollection or recall paradigms in which superior memory for emotional items may be due to the greater semantic interrelatedness of these stimuli (Talmi & Moscovitch, 2004; Talmi, Schimmack, Paterson, & Moscovitch, 2007), the context memory paradigm is not susceptible to the confounding influences of relatedness among contexts. Using the context memory paradigm, we explored effects of brain state (sleep/wakefulness) during retention, emotionality of encoding contexts (negative/neutral), and retrieval task (emotion-relevant/emotion-irrelevant) on context memory and its neural correlates. We predicted superior memory performance and stronger neural responses in regions of known importance for contextual memory such as the hippocampus and parahippocampus (Bar, Aminoff, & Schacter, 2008) at retrieval after sleep. We further predicted that all such effects would be amplified for valenced information, and more apparent in the explicitly emotion-relevant retrieval task. Because sleep and wake groups were tested at different times of the diurnal cycle, we also performed a daytime napping study to control for any impact of circadian variations upon performance.

2. Materials and methods

2.1. Experiment 1—overnight consolidation

2.1.1. Participants

Twenty-two (12 female) healthy right-handed volunteers aged 19–32 years (mean = 24.5 years ± 3.3 SD) and free from any history of sleep pathologies, memory difficulties, or other neurological disorders, were recruited. All participants gave written informed consent and abstained from alcohol and caffeine for 24 h preceding and throughout the study period. The study was approved by the Ethical Review Board at the University of Liverpool.

2.1.2. Task

We used an established contextual memory paradigm (Smith, Dolan, & Rugg, 2004; Smith, Henson, Dolan, & Rugg, 2004; Smith et al., 2005, 2006) in which neutral images of objects (foreground objects) were superimposed upon either negative or neutral background images (encoding contexts) at encoding (see Fig. 1C and below for detail). At test, foreground objects were displayed as cues and participants were asked to retrieve information about the encoding contexts with which these had been initially paired. The test phase consisted of two different task conditions: an emotion-relevant condition (Emotion) and an emotion-irrelevant condition (People). In Emotion, participants indicated whether the encoding context associated with each presented foreground object were emotional or neutral. In People they indicated whether or not the encoding context contained people.

To examine the influence of sleep upon consolidation, a 12-h retention interval was introduced between encoding and the final test session (Fig. 1A). Participants were randomly assigned to two experimental groups: 'Wake' and 'Sleep' with 6 females and 5 males in each group. In the Wake group, Encoding occurred in the morning (9 AM ± 1 h) and Test occurred in the evening (9 PM ± 1 h) such that the retention interval included a normal day during which participants did not sleep. In the Sleep group, however, Encoding occurred in the evening (9 PM ± 1 h) and Test occurred in the morning (9 AM ± 1 h). For this group, the retention interval included a night of sleep (Fig. 1A).

The combination of the two retrieval tasks, the two retention groups, and the two encoding context valences produced a 2 × 2 × 2 design with the factors: task (Emotion/People), group (Sleep/Wake), and encoding context valence (negative/neutral). This allowed comparison of responses associated with the retrieval of negative and neutral memories as a function of both task and retention interval type.

Encoding procedure: Following the method of Smith et al. (2006), each encoding context was shown for 3 s (Fig. 1C) during encoding outside the fMRI scanner. The foreground object was then superimposed on it for five further seconds before both images were replaced with a fixation cross for a further second (Fig. 1C). Participants were asked to form an association between the foreground object and the encoding context, and then press a button. To facilitate learning, the 160 image pairs were separated into two lists of 80, 40 for use in Emotion and 40 for use in People. Importantly, these lists were counterbalanced to contain equal proportions of negative/no people, negative/people, neutral/no people and neutral/people images.

Immediate tests: Immediately after encoding, in order to strengthen memory representations, participants were tested twice with feedback. Here, the learned foreground objects were presented for 2.5 s, followed by a 0.8-s inter-stimulus-interval (ISI). The order of presentation was pseudorandom, and stimuli were equally divided between the two retrieval tasks. In Emotion, there were 3 possible responses: 'old originally paired with a negative encoding context', 'old originally paired with a neutral encoding context', and 'old but I can't remember the encoding context'. In People, the response options were equivalent but indicated whether the encoding context contained people or not rather than whether it was negative or neutral. The two tasks were interleaved in 20 alternating blocks of 10 trials each. A screen stating Emotion or People respectively proceeded each block for 2 s and reminded participants of the task and the three possible responses by listing them in terms of finger position. To strengthen memory of the pairing between foreground objects and encoding contexts, participants were shown the correct encoding context for each object after every response in the immediate test. In order to ensure good performance in the subsequent delayed test in the MRI scanner, participants undertook this immediate test twice with feedback directly after encoding. They took a brief break after completing the second immediate test for the first encoding list, then commenced the same procedure of encoding followed by two immediate tests of the second list. Data from the second immediate test was taken as a measure of pre-consolidation performance.

Testing procedure: Following the 12-h retention interval, participants performed a *Test* session in the MRI scanner. This was similar to the immediate tests described in the Encoding section above, except that no feedback was given. Additionally the learned foreground objects were randomly intermixed with 40 new foreground objects and 80 'null' events in which the crosshair simply stayed on the screen for the 3-s inter trial interval. This created a stochastic distribution of stimulus onset asynchronies, allowing more accurate estimation of responses to stimuli vs. interstimulus baseline (Friston, Zarahn, Josephs, Henson, & Dale, 1999). Finally, in addition to the three response options used during immediate tests (see above), participants could also respond 'new' to indicate that they had not seen a foreground object before. It is noteworthy that this testing procedure, along with the timing of stimulus presentation, was identical to that used by Smith et al. (2006). As with

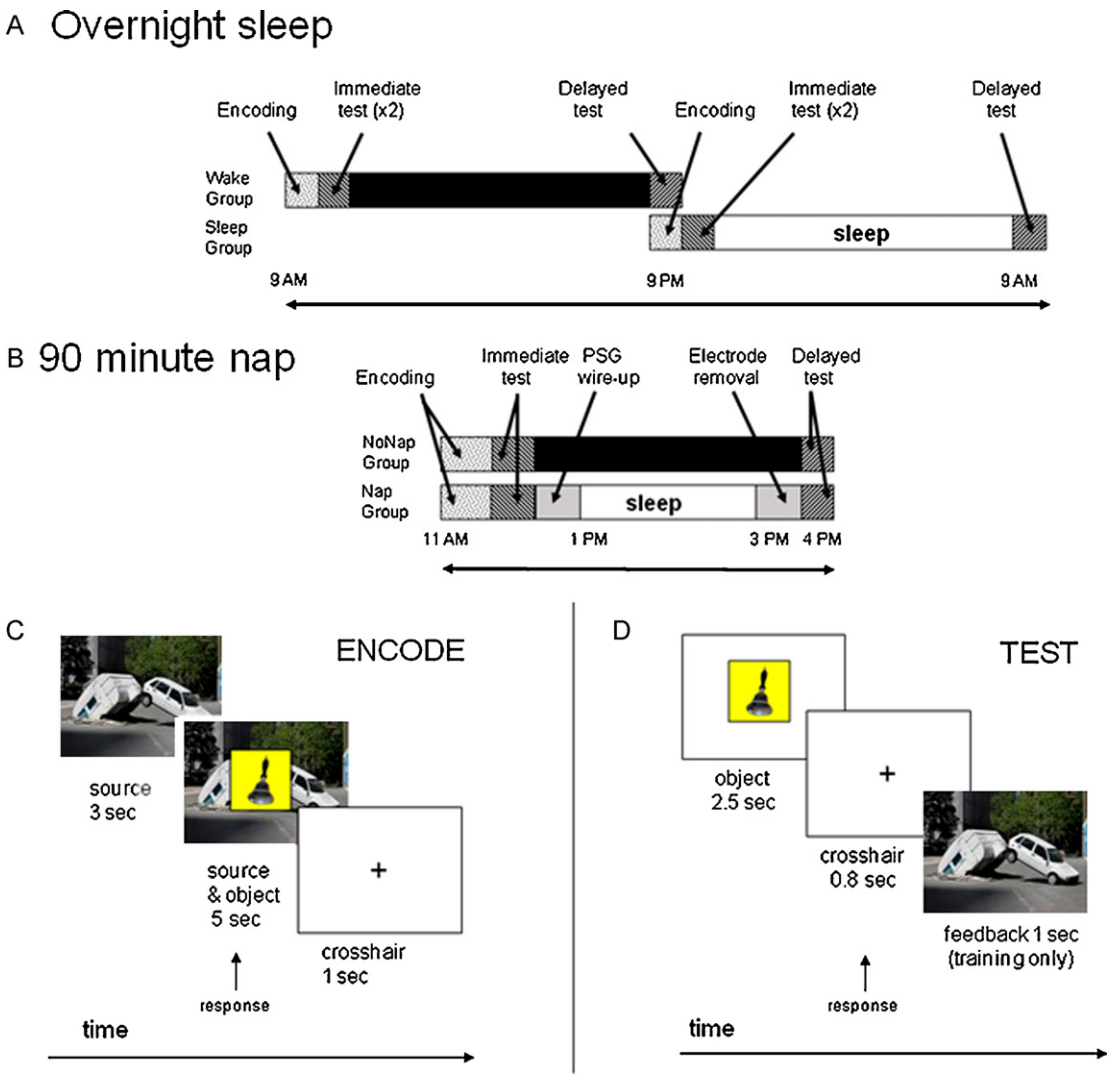

Fig. 1. Experimental paradigm and context memory task. (A) The design of Experiment 1, which used an overnight consolidation delay. Participants were divided into a Wake group trained in the morning and a Sleep group trained in the evening. Each group was tested in the MRI scanner 12 ± 1 h after encoding. The Sleep group therefore consolidated across a night of sleep, while the Wake group consolidated across a day of wakefulness. (B) The design of Experiment 2, which used a daytime napping paradigm. Participants were divided into Nap and Wake groups, these groups were trained and identical times in the day, with the Nap group consolidating across a 90-min nap while the Wake group remained awake. (C) The context memory task (Smith et al., 2006) during Encoding participants viewed a context picture for 3 s before a foreground object was superimposed on it for a further 5 s. Participants formed an association between the encoding context and the foreground object, then responded with a button press. At Test (D) foreground objects were shown for 2.5 s, followed by a crosshair for 0.8 s. Testing was divided into two tasks: Emotion and People. In Emotion, there were 3 possible responses: old originally paired with a negative encoding context, old originally paired with a neutral encoding context, and old but I cannot remember the encoding context. In People the response options were equivalent but participants indicated whether the encoding context contained people or not rather than whether it was negative or neutral. Training included two tests with feedback in which the encoding context was displayed after the subject had responded. Delayed testing (after the retention period) was carried out in the MRI scanner and did not include feedback. In Delayed testing, learned foreground objects were intermixed with novel (unlearned) foreground objects, and participants had an additional response option 'new' in both tasks.

Encoding, the Test session was split into equal halves. Data were collected in two separate fMRI runs, with a brief resting break in between (participants remained in the scanner).

2.1.3. Analysis of behavioural data

Behavioural performance was assessed using correctly attributed encoding contexts (context memory) and correctly recognised foreground objects (object recognition). Object recognition was quantified by combining context memory with items in which the foreground object was correctly remembered but the encoding context was wrong and items in which the foreground object was remembered but encoding context was unknown. Forgetting was measured as the performance change between immediate and delayed memory tests (forgetting = immediate – delayed) in terms of both context memory (context forgetting) and object recognition (object forgetting). Our analysis used a combination of ANOVAs and *t*-tests, with a two-tailed $p < 0.05$ considered as significant.

During analysis, objects from both People and Emotion tasks were divided, on the basis of whether or not the encoding context with which they were associated was negative. The Emotion task measured the impact of an emotional encoding context upon subsequent memory of explicitly emotional information about this context, while the People task measured the impact of an emotional encoding context upon subsequent memory for neutral information about this context (the presence/absence of people). The People task can therefore be thought of as a measure of implicitly emotional memory.

2.1.4. Stimuli

Encoding contexts were photographs taken from the IAPS battery (Lang, Bradley, & Cuthbert, 2005) (negative items were among the most strongly valenced images in the battery) and supplemented with images from the internet. Pictures ranged from everyday scenes, to images of injury, violence, decay and contaminated foods. 160 photographs were used as encoding contexts and were composed from four equal categories: neutral with people, neutral without people, negative with people, and negative without people. The 320 neutral foreground objects were taken from the Hemera objects collection, http://desktoppub.about.com/cs/stockphotovendors/gr/photoobjects1-2.htm, and appeared on a square yellow background. Eight unique sets of pairings between foreground objects and encoding context photographs were created pseudorandomly, avoiding pairings where a semantic relationship could easily be produced between the foreground object and encoding context. The eight encoding lists were

presented in a random order, counterbalanced across participants (Smith et al., 2006).

2.1.5. MRI scanning

Scanning was performed using a 3-T Trio MRI scanner (Siemens Vision, Erlangen, Germany) with an 8 channel head coil. Stimuli were back-projected onto a screen at the rear of the magnet bore and viewed via an angled mirror attached to the head-coil. Responses were made using a custom-built button box which recorded these with accuracy of ~1 ms.

2.1.6. Imaging parameters

T2-weighted echo planar images (EPI) with BOLD (blood-oxygen-level-dependent) contrast were acquired using a specialized sequence which minimized signal dropout in the medial temporal lobe (Deichmann, Gottfried, Hutton, & Turner, 2003). We used the following scanning parameters to achieve whole brain coverage: 33 oblique axial slices at a 20° tilt in the anterior–posterior axis, TR of 2 s, slice thickness of 2 mm (80% gap), TE of 30 ms, in plane resolution was 3.5 mm × 3.5 mm. Data were collected in two separate sessions (runs). Each session lasted 9 min, giving 270 volumes. High resolution anatomical whole brain images were obtained using a T1 weighted 3D-gradient-echo pulse sequence, with the following parameters: (T1 190, TR 7.92, TE 2.48, FOV 224 × 256, matrix 256 × 256 × 256 pixels, flip angle 16) acquired in sagittal plane.

2.1.7. fMRI processing

Functional MRI images were analysed using the statistical parametric mapping (SPM2) software package (Wellcome Trust Centre for Neuroimaging London, UK, http://www.fil.ion.ucl.ac.uk/spm). After the first three volumes of each session were discarded to allow for T1 equilibration effects, images were corrected for head motion by realigning with the first image of the first session and spatially normalised to an EPI template corresponding to the Montreal Neurological Institute (MNI) brain. Normalised images were smoothed using a Gaussian Kernel size with a full width at half-maximum (FWHM) of 8 mm.

fMRI analysis: To characterise functional responses, data were examined using a two-level random effects analysis. At the first level, the event-related design matrix contained regressors for: context memory, items in which the participant correctly recognized an old foreground object but attributed the encoding context incorrectly, items in which the participant correctly recognized an old foreground object but indicated that they did not remember the encoding context, and misses. These regressors were included separately for each valence (neutral and negative encoding contexts) and for each task (Emotion and People). Correct rejections were also modelled separately for each task. To control for motion artefacts, six rigid body movement parameters were included as regressors of no interest. Parameter estimates reflecting the height of the hemodynamic response function for each regressor were calculated at each voxel. Contrast images relating to specific combinations of correctly classified items were calculated. These included (a) negative context memory, (b) neutral context memory, (c) correct rejections, and (d) direct comparison of context memory across valences (negative context memory > neutral context memory). These four contrasts were computed separately for data from Emotion, data from People, and for data pooled across both tasks.

The resulting contrast images were entered into two second-level random effects ANOVA analyses. The first such analysis (contrast 1) examined the main impact of retention type (sleep vs. wake) upon context retrieval. Context retrieval included both neutral and negative items and was calculated as context retrieval = [all context memory > all correct rejections]. In calculating context retrieval, the subtraction of correct rejections provided two functions. First, it controlled for circadian factors by removing activities associated with retrieval at a specific time of day following the method of (Walker, Stickgold, Alsop, Gaab, & Schlaug, 2005). Second, it allowed separation of context retrieval responses from those indexing stimulus processing. To determine the impact of retention type upon these responses context retrieval was compared across Sleep and Wake groups. Specifically, contrast 1 = [Sleep (context retrieval) < > Wake (context retrieval)]. To constrain sleep-related findings to the episodic memory system, the results of this contrast were inclusively masked by the main effect of context retrieval (all context memory > all correct rejections) in both Sleep and Wake groups at $p = 0.05$ uncorrected, see Fig. S1 and Table S1A of the supplementary material. The second contrast (contrast 2) isolated brain responses specifically associated with overnight changes in processing negative emotional memories. This was achieved by calculating the interaction: [Sleep (negative context memory > neutral context memory) < > Wake (negative context memory > neutral context memory)] (contrast 2). Here, the subtraction of neutral context memory from negative context memory controlled for circadian factors by removing activities associated with retrieval at a specific time of day and isolated effects associated with retrieval of negative emotional items rather than with retrieval in general. To constrain findings to areas associated with emotional processing, the results of this contrast were inclusively masked by the main effect of valence on context memory (negative context memory > neutral context memory), see Fig. S2 and Table S1B of the supplementary material) at $p = 0.05$ uncorrected. To examine the influence of retrieval task, both contrasts were calculated first using data pooled across both tasks, next using data from Emotion, and third using data from People. Finally, task-specific effects were tested by comparing contrasts across tasks, e.g. using Emotion (contrast 1 or 2) < > People (contrast 1 or 2). We followed a well established approach in which clusters of $K = 10$ or more voxels at $p < 0.001$ were considered significant.

Connectivity analysis: Functional connectivity was assessed using the psychophysiological interaction (PPI) analysis to evaluate how activity between brain regions covaries in relation to task demands (Friston et al., 1997; Gitelman, Penny, Ashburner, & Friston, 2003). We used the PPI to determine whether functional connectivity between our seed region and other brain areas was more strongly modulated by emotion in participants who slept during the retention interval than in participants who remained awake. SPM2 was used to extract the effects of interest time series for our seed region, which fell in the peak voxel the right parahippocampus (4 mm radius sphere centred on *x,y,z*; 24, −16, −20, identified in contrast 2, Fig. 4C), this was the physiological effect. Next, the product of this time course and the contrast (negative context memory > neutral context memory), our psychological factor, was calculated, to create the psychophysiological interaction (PPI) term. A first level design matrix was then constructed for each participant using three regressors: (i) the physiological factor, (ii) the psychological factor, and (iii) the interaction between the first and the second regressors (PPI). To control for motion artefacts, six rigid body movement parameters were included as regressors of no interest. Contrasts for the interaction term (PPI) revealed brain regions considered to covary with the parahippocampal seed region. These connectivity contrasts were then taken through to a second-level, random-effects analysis where we tested for differences between Sleep and Wake groups. As previously, data were thresholded at $p = 0.001$ uncorrected and clusters of 10 or more contiguous voxels ($K = 10$) are reported (see Table 2). The PPI analysis was performed three times: using data pooled across tasks, using Emotion task data, and using People task data.

2.2. Experiment 2—daytime napping

Because the Sleep and Wake groups in Experiment 1 were trained and tested at different times of day (see Fig. 1A), between group performance differences could potentially have resulted from circadian factors rather than differential consolidation across wake and sleep. To control for this possibility, we performed a second experiment in which participants from Nap and Wake groups were trained and tested at equivalent times of day (11 AM and 4 PM), with the Nap group obtaining a daytime nap between training and testing, while the Wake group remained awake throughout this interval (see Fig. 1B). Further details of the experiment are given below.

2.2.1. Participants

Thirty-eight (28 female) healthy volunteers aged 18–34 years (mean = 20.9 years ± 3.7 SEM) and free from any history of sleep pathologies, memory difficulties, or other neurological disorders, were recruited for this experiment. Psychology undergraduates took part in exchange for course credit, whereas other participants were paid £15. All participants gave written informed consent in line with the School of Psychological Sciences Research Ethics Committee at the University of Manchester. All participants were free of any history of sleep pathologies, memory difficulties, or other neurological disorders. Furthermore, participants abstained from alcohol and caffeine for 24 h preceding and throughout the study period.

2.2.2. Paradigm

Participants were randomly assigned to Wake and Nap groups. Each group contained 19 participants comprising 14 females and 5 males. For both groups, encoding began at 11 AM and the delayed test at 4 PM (Fig. 1B). After the immediate test, participants in the Wake group were free to go about their usual daytime activities until they returned at 4 PM. Participants in the Nap group remained in the Manchester Sleep Laboratory, where they were wired up for polysomnography (approximately 1 h), then given an opportunity to nap comfortably from 1 PM to 3 PM. After awakening, they were allowed time to remove the electrodes and recover from sleep inertia before the delayed test commenced at 4 PM. Together, the two retention groups and two encoding context valences produced a 2 × 2 mixed design with the between subject factor participant group (Wake/Nap) and the within subjects factor encoding context valence (negative/neutral).

2.2.3. Task

Experiment 2 used the same context memory paradigm as Experiment 1 (Smith, Dolan, et al., 2004; Smith, Henson, et al., 2004; Smith et al., 2005, 2006) but with several minor alterations. To facilitate deep encoding of emotional contexts, participants rated each encoding context on a scale of 1 (highly negative) through 9 (highly positive) before forming an association between foreground object and encoding context. Because both Emotion and People tasks showed the same pattern of behavioural results in Experiment 1, only the Emotion task was used at test in Experiment 2. In this task, participants indicated whether or not each presented foreground object had been paired with an emotional encoding context.

Because we did not perform fMRI in Experiment 2, there was no need to ensure the high level of response accuracy which was required in Experiment 1. The immediate test was therefore performed only once and did not include feedback. Instead, it followed the same procedure as the delayed test in Experiment 1, with 20% new foreground objects pseudorandomly intermixed with the learned foreground objects (different 'new' foreground objects were used for immediate and delayed tests).

Table 1
Descriptive statistics for Experiments 1 and 2. The standard deviation for each category is shown below the mean. In the column heads, 'neg' indicates a negative encoding context and 'neut' indicates a neutral encoding context.

(A) **Experiment 1**

	Emotion Task				People task			
	Sleep		Wake		Sleep		Wake	
	Neg	Neut	Neg	Neut	Neg	Neut	Neg	Neut
	Context memory							
Immediate	30.1 (1.6)	31.3 (1.7)	29.7 (1.7)	30.9 (0.9)	31.5 (1.8)	32.1 (1.6)	29.0 (1.2)	31.0 (2.0)
Delayed	28.3 (4.2)	28.8 (4.8)	24.5 (8.4)	24.8 (8.0)	28.6 (5.5)	27.5 (6.5)	25.8 (5.2)	25.1 (6.8)
	Correct object, incorrect context							
Immediate	9.4 (5.1)	8.1 (5.8)	9.6 (5.4)	8.5 (2.7)	8.2 (5.5)	7.3 (5.2)	9.4 (5.1)	8.1 (5.8)
Delayed	8.6 (0.6)	7.7 (1.0)	10.6 (1.9)	8.7 (1.4)	8.7 (1.0)	7.2 (1.1)	9.6 (1.1)	8.2 (1.5)
	Correct object, don't know context							
Immediate	0.4 (0.7)	0.2 (0.4)	0.4 (0.7)	0.5 (0.7)	0.3 (0.7)	0.5 (1.0)	0.4 (0.7)	0.2 (0.4)
Delayed	1.1 (1.4)	1.4 (1.4)	1.4 (1.8)	1.5 (1.5)	1.0 (1.2)	2.4 (2.1)	1.1 (1.4)	1.4 (1.4)
	Context false alarms							
Immediate	–	–	–	–	–	–	–	–
Delayed	0.1 (0.3)	1.5 (1.9)	0.8 (0.9)	2.1 (2.2)	0.5 (0.5)	0.5 (0.7)	0.3 (0.5)	1.2 (1.3)
	Object recognition							
Immediate	39.9 (0.3)	39.6 (7.3)	39.7 (0.9)	39.9 (0.3)	40.0 (0.0)	39.9 (0.3)	40.0 (0.0)	39.8 (0.6)
Delayed	38.0 (2.3)	37.9 (2.9)	36.5 (3.4)	35.1 (6.6)	38.4 (2.5)	37.1 (4.2)	36.8 (3.7)	35.5 (4.3)

(B) Experiment 2

	Emotion task			
	Nap		Wake	
	Neg	Neut	Neg	Neut
	Context memory			
Immediate	45.2 (12.1)	40.2 (15.1)	44.3 (13.0)	35.7 (13.1)
Delayed	42.8 (10.9)	38.4 (13.4)	39.4 (11.8)	31.1 (11.5)
	Correct object, incorrect context			
Immediate	12.1 (8.8)	11.1 (5.8)	9.6 (4.9)	16.4 (9.1)
Delayed	12.7 (11.4)	11.5 (6.3)	10.1 (5.0)	15.9 (0.3)
	Correct object, don't know context			
Immediate	13.2 (8.8)	16.5 (11.3)	12.5 (7.9)	13.9 (8.4)
Delayed	17.6 (10.5)	21.5 (12.2)	18.4 (9.9)	21.5 (12.3)
	Context false alarms			
Immediate	0.1 (0.2)	0.6 (0.8)	0.8 (1.2)	1.0 (1.2)
Delayed	0.4 (0.8)	0.7 (2.1)	0.4 (0.6)	0.8 (1.0)
	Object recognition			
Immediate	70.5 (6.1)	67.8 (7.1)	66.4 (8.8)	66.0 (9.4)
Delayed	73.2 (4.6)	71.4 (6.8)	67.9 (10.0)	68.5 (9.6)

This inclusion of new items in the immediate test allowed a more accurate measure of immediate performance since participants had four possible response options, the presented foreground object is: 'new', 'old originally paired with a negative encoding context', 'old originally paired with a neutral encoding context', or 'old but I can't remember the encoding context'. Data were analysed using the same method as in Experiment 1.

3. Results

3.1. Experiment 1—overnight consolidation

3.1.1. Behaviour

Context memory was 77% correct (±SD 13%) at the immediate test, and 61% correct (±SD 16%) following the offline consolidation delay when data were pooled across negative and neutral items and across tasks. This was significantly higher than chance (25%), one-sample T-test $p < 0.001$ in both cases. Object recognition was 99.6% correct (±SD 16%) at the immediate test, and 92.3% correct (±SD 10%), at the delayed test when data were pooled in the same way. See Table 1(A) for further descriptives.

Performance at the immediate test prior to consolidation, was equivalent in Sleep and Wake groups (Fig. 2A). A pair of $2 \times 2 \times 2$ mixed ANOVAs modelling task (Emotion/People), encoding context valence (negative/neutral), and participant group (Sleep/Wake) showed no significant effects. Because there was no effect of retrieval task on either context memory ($F(20) = 0.68$; $p = 0.42$) or object recognition ($F(20) = 0.71$; $p = 0.14$) this factor was merged within a 2×2 ANOVA of valence (negative/neutral) and group (Sleep/Wake), but the merged ANOVA revealed no significant findings. Since the Sleep group encoded in the evening, while the Wake group encoded in the morning, these null results suggest that time of day had no significant impact upon encoding or immediate recall in either context memory or object recognition.

To quantify the impact an off-line delay upon memory performance, we created a measure of forgetting which was calculated for each participant as forgetting = immediate performance − delayed performance (Payne et al., 2008). This was first examined using the $2 \times 2 \times 2$ ANOVAs described above. Because there was no effect of retrieval task on forgetting in either context memory ($F(20) = 0.10$; $p = 0.75$) or object recognition ($F(20) = 1.36$; $p = 0.72$) the task factor was then merged within a 2×2 ANOVA as in the immediate test (see above). In context memory, this merged ANOVA showed that participants who slept overnight during the retention period forgot less encoding contexts than participants who remained awake ($F(42) = 4.88$; $p = 0.03$; Fig. 2B). There was also an effect of

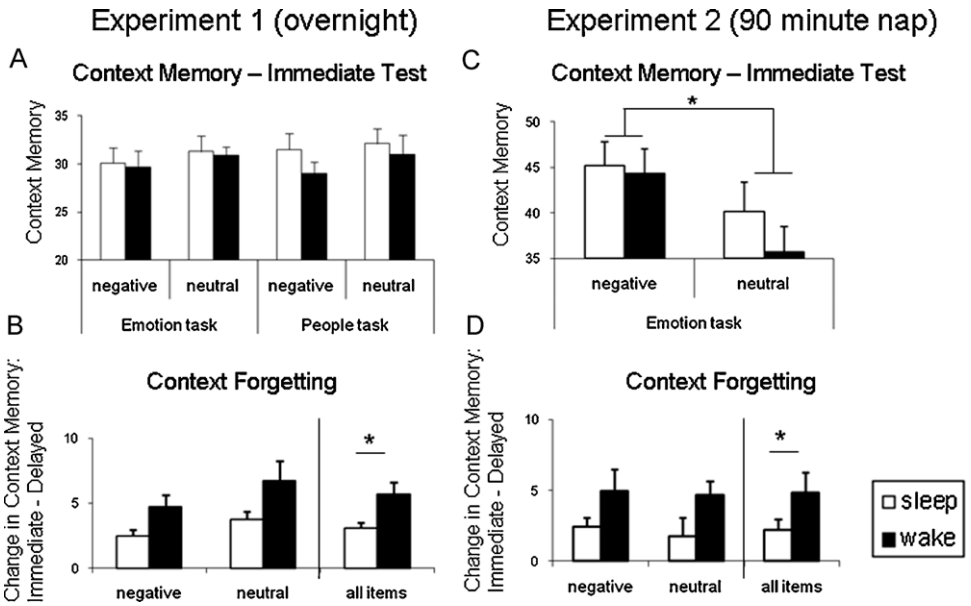

Fig. 2. Behavioural performance on the context memory task. At the immediate test, the number of correctly attributed contexts (context memory) did not differ between groups (Sleep/Wake), encoding valences (negative/neutral), or tasks (Emotion/People) in either Experiment 1 (A) or Experiment 2 (C). The number of contexts forgotten across the retention interval (context forgetting) did, however, differ between groups. Participants who slept during the retention interval showed less context forgetting in both Experiment 1 (B) and Experiment 2 (D). An asterisk (*) indicates significance at $p < 0.05$. Error bars show 1 SEM.

valence, with negative encoding contexts less likely to be forgotten ($F(42) = 5.87$; $p = 0.02$), however there was no interaction between sleep and valence ($F(42) = .29$; $p = 0.59$). The 2 × 2 ANOVA revealed no significant effects on object recognition.

In summary, both context memory and object recognition were equivalent for Sleep and Wake groups immediately before the retention interval, indicating similar levels of memory at baseline and showing that performance was not influenced by the time of day of training or testing. At the subsequent delayed test however, participants who had slept forgot less context information than participants who had remained awake. There was no interaction between emotional valence and this sleep-related modulation of context forgetting.

3.1.2. Functional imaging

In the fMRI data, we first searched for regions of the episodic memory system in which context retrieval responses differed after consolidation across wake and sleep. Pooling the results of contrast 1 [Sleep (context retrieval) < > Wake (context retrieval)] across both Emotion and People tasks showed that the superior behavioural performance following sleep was associated with enhanced responses in the left superior parietal cortex, and left hippocampus (to avoid performance confounds we considered only correct context memory trials). This effect was amplified for the Emotion task compared to the People task though direct comparison revealed no significant difference Table 2(A and B) and Fig. 3. No area was more active in Wake than Sleep in any of the above contrasts.

The interaction between emotional valence and retention type (Sleep/Wakefulness) was examined using contrast 2. Valence impacted on neural activity only when the task demanded explicit recollection of context emotionality (Emotion task). No effect was observed for the pooled Emotion and People tasks, nor for the People task alone, yet for the Emotion task greater responses were

Table 2
Results from contrast 1 (main effect of sleep on context retrieval) calculated with data from the Emotion task (A), and with data from both tasks (B). These results were inclusively masked by the main effect of context retrieval. Results from contrast 2 (Sleep × Valence interaction) calculated with data from the Emotion task (C). These results were inclusively masked by the main effect of valence on context memory. Results from a psychophysiological interaction analysis (PPI) seeded at the peak response in (C) [24, −16, −20] are listed in (D). Clusters of 10 or more voxels were considered significant at $p < 0.001$ uncorrected.

No. of voxels	*T*	*Z*	Probability	*x,y,z* (mm)	Region
(A) Emotion task: Sleep (context retrieval) > Wake (context retrieval)					
183	5.5	4.3	<0.001	−18 −60 40	Superior parietal
10	5.5	4.2	<0.001	2 −32 −50	Medulla
33	5.0	4.0	<0.001	−26 −24 −12	Hippocampus
(B) Both tasks: Sleep (context retrieval) > Wake (context retrieval)					
54	6.7	4.8	<0.001	−12 −34 26	Posterior cingulate
154	5.3	4.2	<0.001	−18 −60 40	Superior parietal
13	4.9	4.0	<0.001	−26 −24 −12	Hippocampus
(C) Emotion task: Sleep × Valence					
31	6.6	4.8	<0.001	24 −16 −20	Parahippocampus
43	5.2	4.1	<0.001	−8 −34 30	Posterior cingulate
12	4.4	3.6	<0.001	−30 −6 −24	Amygdala
11	4.3	3.6	<0.001	6 44 −14	Ventromedial prefrontal
10	3.7	3.2	<0.001	2 −40 38	Precuneus
(D) Both tasks: PPI seeded on 24 −16 −20, contrast: Sleep × Valence					
22	4.4	3.6	<0.001	−28 −6 −32	Amygdala/periamygdala
15	4.3	3.6	<0.001	30 −4 −28	Amygdala/periamygdala
12	4.1	3.4	<0.001	−8 58 26	Dorsomedial prefrontal cortex

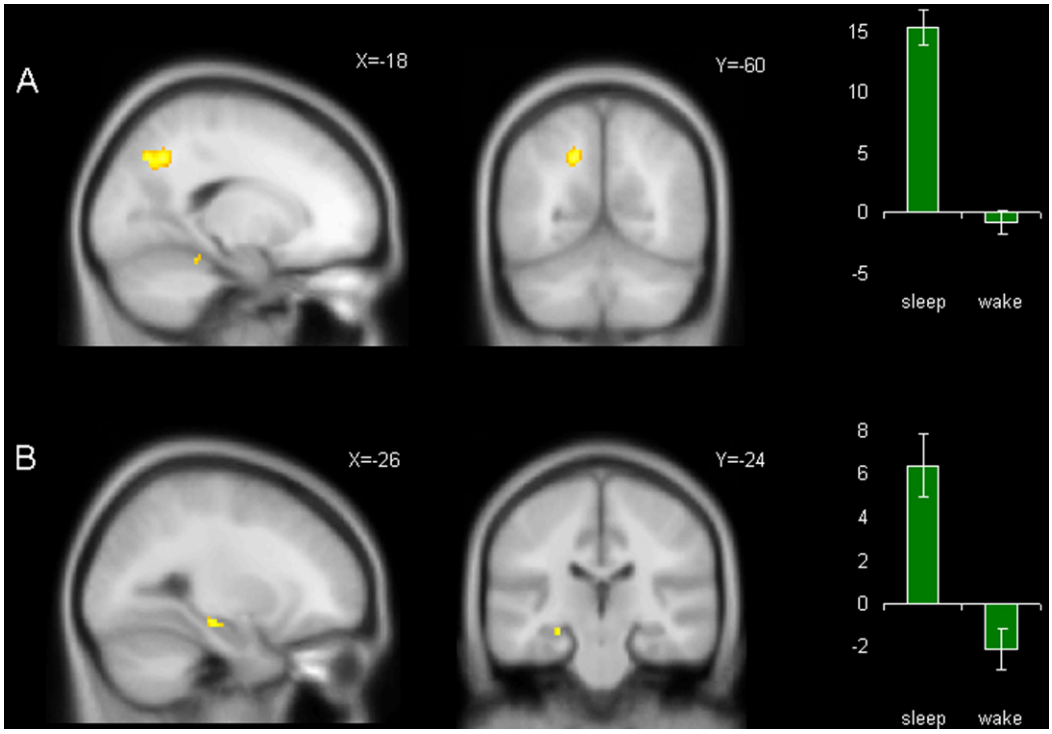

Fig. 3. Main effect of sleep on context retrieval. The figure shows the results of contrast 1 [Sleep (all context memory > all correct rejections) > Wake (all context memory > all correct rejections)] calculated using data from both Emotion and People tasks and masked by the main effect of context retrieval. (A) Shows the superior parietal response while (B) shows the left hippocampal response. Both activations are depicted in sagittal and coronal views, with parameter estimates for the peak voxel shown to the right, error bars are ±1 SEM. Responses are rendered onto the MNI 152 brain at $p < 0.001$ uncorrected and an extent threshold of $K = 10$.

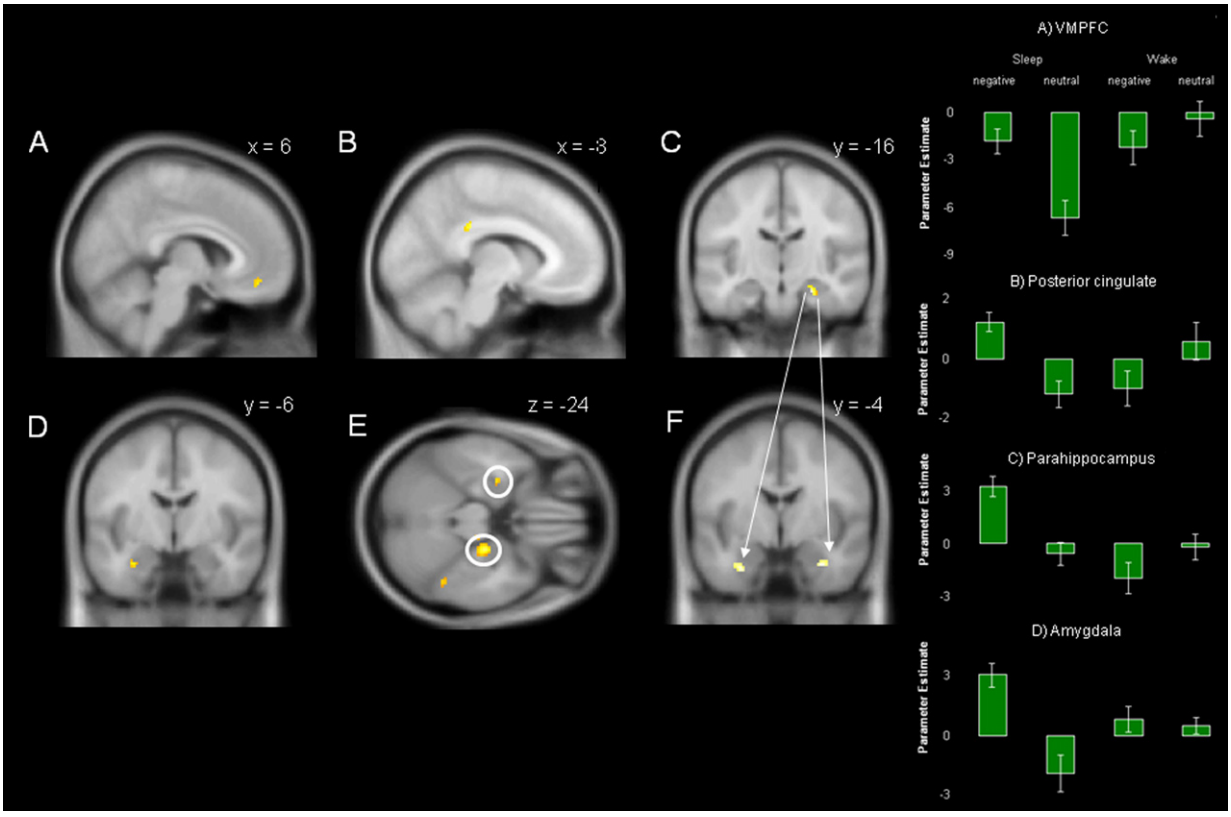

Fig. 4. Interaction between sleep and valence. The figure shows the results of contrast 2 [Sleep (negative context memory > neutral context memory) > Wake (negative context memory > neutral context memory)] calculated using data from the Emotion task and masked by the main effect of valence on context memory. Depicted responses fall in (A) ventromedial prefrontal cortex, (B) posterior cingulate, (C) right hemispheric parahippocampus, and (D) left hemispheric amygdala. (E) Shows an axial view of both parahippocampus and amygdala responses. Parameter estimates for each response are shown to the right, error bars are ±1 SEM. A psychophysiological interaction (PPI) analysis seeded at the peak of parahippocampal response at [24, −16, −20] reveals significantly enhanced functional connectivity between this region and the bilateral amygdala/periamygdala (F). Responses are overlaid on the MNI 152 brain at $p < 0.001$ uncorrected and an extent threshold of $K = 10$.

observed in the Sleep group as compared to the Wake group within five distinct regions. The strongest of these occurred in right anterior parahippocampus, but significant responses were also observed in left amygdala, ventromedial prefrontal cortex, posterior cingulate (abutting retrosplenial cortex), and precuneus, Fig. 4A–D and Table 2(C). No area was more active in Wake than Sleep in any of the above contrasts.

Altered connectivity between the hippocampal complex and amygdala has been suggested to result from consolidation during sleep (Hu et al., 2006; Wagner et al., 2005, 2006). To explore this possibility in context memory, we applied a psychophysiological interaction (PPI) analysis (Friston et al., 1997; Gitelman et al., 2003) to examine functional coupling between our seed region and the rest of the brain as a function of the interaction between sleep and valence (see Section 2). We chose the right parahippocampus at 24/−16/−20 as a seed region because it showed a greater enhancement in response to the interaction (contrast 2) in the Emotion task than any other brain area, see Table 2(C). Pooling Emotion and People tasks, we observed significantly greater functional connectivity between this right parahippocampal seed and the bilateral amygdala/periamygdala in the Sleep group as compared to the Wake group during correct attribution of valenced contexts, Fig. 4E and Table 2(D). For the purpose of precise localisation, the PPI response was overlaid on a probabilistic cytoarchitectonic maximum probability map (MPM) using the SPM Anatomy toolbox (Version 1.4, http://www.fz-juelich.de/ime/spm_anatomy_toolbox (Eickhoff et al., 2005)). This assigned the left hemispheric response to basolateral amygdala with a probability of 60%, and the right hemispheric response to amygdala with a probability of 100%. Neither separate analysis of Emotion and People nor direct comparison of these conditions revealed significant findings. These results demonstrate greater functional coupling between the parahippocampal and amygdala regions during successful emotional memory retrieval following overnight consolidation.

Overall our functional data show that the post-sleep reduction in context forgetting is paralleled by stronger responses in hippocampus and superior parietal cortex at retrieval. Additionally, we show stronger functional responses in the emotional memory system, as well as increases in connectivity within that system, in association with the interaction between sleep and valence.

3.2. Experiment 2—daytime napping

In order to confirm that the reduced forgetting observed after sleep in Experiment 2 was not due to circadian differences between the times at which Sleep and Wake groups were trained or tested, we conducted Experiment 2 in which Wake and Nap groups were trained and tested at the same time of day. These experimental groups showed comparable performance at the immediate test, see Table 1(B) for descriptives. A 2 × 2 mixed ANOVA with the between subject factor participant group (Wake/Nap) and the within subject factor encoding context valence (negative/neutral) showed no difference between groups in terms of either context memory (Fig. 2C) or object recognition. There was a main effect of valence in both measures, with negative encoding contexts remembered better than neutral encoding contexts ($F(36) = 11.69$; $p = 0.002$), and foreground objects associated with a negative encoding context remembered better than those associated with a neutral encoding context ($F(36) = 8.15$; $p = 0.007$). There was also a significant interaction between group and valence in object recognition, with negatively associated foreground objects enjoying a greater advantage in the Nap group than in the Wake group ($F(36) = 4.33$; $p = 0.045$).

As in Experiment 1, the impact of retention upon context memory performance was quantified using forgetting (forgetting = immediate performance − delayed performance) (Payne et al., 2008). The 2 × 2 mixed ANOVA described above indicated that participants who slept during the retention period forgot fewer encoding contexts than participants who remained awake ($F(36) = 5.51$; $p = 0.024$) see Fig. 2D, however there was no main effect of context valence ($F(36) = 0.09$; $p = 0.77$) and no interaction between factors ($F(36) = 0.02$; $p = 0.90$). Analysis of object recognition revealed no significant findings.

To summarise results from Experiment 2, context memory and object recognition were equivalent for Wake and Nap groups immediately before the retention interval. After retention however, participants who slept forgot less contextual information than participants who remained awake. This replicates the main behavioural result of the Experiment 1 and, because there was no difference in the diurnal times of training and testing for Wake and Nap groups in Experiment 2, these findings greatly reduce the possibility that the results of Experiment 1 could have occurred due to circadian factors, suggesting instead that they relate to sleep obtained during the retention interval.

4. Discussion

We examined context memory retrieval after 12 h of consolidation across either daytime wake or overnight sleep. Our design included both emotional and neutral encoding contexts, allowing examination of how encoding context valence interacts with sleep-related consolidation. Our data show that context memory decayed less across sleep than across wakefulness, and that superior post-sleep performance was linked to stronger responses in the left hemispheric hippocampus and superior parietal cortex. Interestingly, sleep protected emotional and neutral context memories to the same extent, though our fMRI data show a functional interaction between context valence and sleep, with areas of the emotional memory system significantly more activated, and more strongly interconnected, during correct retrieval of negative encoding contexts post-sleep. This difference between functional and behavioural results could be due to differences in the way sleep impacts upon context and recognition memory—a full discussion is provided below.

4.1. Main effect of overnight retention

Our data show significantly stronger responses in the hippocampus and superior parietal cortex during correct context retrieval after a 12-h retention interval containing sleep compared to an equivalent time period of daytime wakefulness (Fig. 2B). Because these structures are core components of the episodic memory system, and because they are strongly linked to memory retrieval (Cabeza, 2008; Cabeza, Ciaramelli, Olson, & Moscovitch, 2008) the more robust functional responses observed post-sleep are very likely associated with altered processing in that system. Importantly, these enhancements occurred irrespective of the emotionality of remembered information, and irrespective of retrieval task.

A number of prior studies have demonstrated enhanced hippocampal responses during memory retrieval or performance of a learned skill after retention across sleep compared to retention across natural wake (Albouy et al., 2008; Walker et al., 2005) or overnight sleep deprivation (Gais et al., 2007; Sterpenich et al., 2007, 2009). The current findings extend this literature to include context memory. Because the hippocampus is critical for contextual binding (Davachi & Wagner, 2002; Giovanello, Verfaellie, & Keane, 2003; Jackson & Schacter, 2004; Shoqeirat & Mayes, 1991) our result could suggest that such responses are associated with greater memory for contextual detail after retention across sleep as compared to wake. Such effects are attributable either to passive protection of memories, whereby hippocampal representations do not decay as dramatically across sleep as they do across wakeful-

ness, or to active enhancement of such representations by sleep, see (Ellenbogen, Payne, & Stickgold, 2006).

Unlike the hippocampal response, the stronger activation we observed in superior parietal cortex after sleep is most likely specific to the context memory task. Parietal cortex responds more in context memory than in item-memory irrespective of whether information is correctly retrieved (Dobbins, Foley, Schacter, & Wagner, 2002; Dobbins, Rice, Wagner, & Schacter, 2003; Dobbins & Wagner, 2005), and could therefore mediate attempts to remember an encoding context instead of actual recollection of this context. Two closely related models (Cabeza, 2008; Cabeza et al., 2008; Ciaramelli, Grady, & Moscovitch, 2008; Ciaramelli, Grady, Levine, Ween, & Moscovitch, 2010) propose that dorsal parietal cortex is responsible for top-down direction of attention for mnemonic search in difficult memory problems. Because sleep facilitates the reorganisation of mnemonic representations, for instance by integrating new learning into existing knowledge (Dumay & Gaskell, 2007), forming generalised (Pace-Schott et al., 2009) or holistic (Ellenbogen et al., 2006) representation of newly learned information, and downscaling of evoked EEG potentials to context memory (Verleger, Ludwig, Kolev, Yordanova, & Wagner, 2011), the parietal responses observed here could be associated with differences in the way the memory for contextual information is organised or accessed after sleep, with a resultant impact on memory search.

4.2. Interaction between overnight retention and valence

Based on the literature showing emotion-specific memory enhancements after sleep (Hu et al., 2006; Nishida et al., 2009; Payne et al., 2008; Payne & Kensinger, 2011; Sterpenich et al., 2007, 2009; Wagner et al., 2005, 2006) we expected to find an interaction between sleep and valence, with sleep exerting a greater protective influence on memory for emotional contexts than for neutral ones. Interestingly, our behavioural data did not follow this pattern. In both Experiments 1 and 2 we found less context forgetting after sleep than after wake, but no interaction between this reduction and context valence. Because this result differs markedly from the findings of tasks such as the Recollection/Familiarity paradigm (Hu et al., 2006; Nishida et al., 2009) and tests of memory for details in emotional texts (Wagner et al., 2005, 2006) or pictures (Payne et al., 2008; Payne & Kensinger, 2011) it suggests that the behavioural component of the context memory task does not probe those aspects of emotional memory which are selectively facilitated by sleep. Thus, while the prior literature (Payne et al., 2008; Payne & Kensinger, 2011) suggests that memory for emotional details embedded within learned images is enhanced by sleep, our data show that the associative link between an emotional context and a neutral foreground object is not strengthened in this way. This also explains why our behavioural findings with respect to the influence of sleep were equivalent for both explicitly emotional (Emotion task) and implicitly emotional (People task) context memory, since context emotionality did not interact with the influence of sleep in either case.

A differential impact of sleep upon emotional context memory and emotional recall is in line with observations that the sense of vividness evoked by emotional memory can be dissociated from memory for contextual details (Kensinger & Schacter, 2008; Sharot & Yonelinas, 2008). The specificity of the functional interaction we observed between sleep and valence to the emotion task (in which responses related to the emotionality of encoding contexts) is in keeping with the possibility that sleep selectively enhances memory for emotional details in the encoding context, but not for the link between that context and the neutral foreground object. Thus the Emotion task may have triggered memory for details about the emotional encoding context to a greater extent than the People task (in which responses were not influenced by emotionality). A close match between the responses in left amygdala, ventromedial prefrontal cortex, and cingulate cortex which were observed during emotional memory after sleep in the Emotion task, and those which responded to an equivalent contrast in a recent study of how sleep impacts upon memory for emotional details in otherwise neutral pictures (Payne & Kensinger, 2011) further corroborates this account. Additionally, several elegant studies (Dolcos, LaBar, & Cabeza, 2005; Smith et al., 2006) suggest a recursive relationship between amygdala and hippocampus during recollection, wherein hippocampus-mediated memory retrieval enhances emotion-related responses in the amygdala, and these emotion-related responses in turn stimulate memory for further detail. The enhanced connectivity which we observed between parahippocampus and bilateral amygdala provides a clear link between this proposal and the current dataset.

Turning to our functional results, the current observations reinforce those of Payne and Kensinger (2011) by showing stronger neural responses in parts of the emotional memory system, including left amygdala, ventromedial prefrontal cortex, and cingulate during emotional memory after sleep. Because the context memory paradigm is protected both against the confounding influence of semantic interrelatedness among emotional stimuli (which can lead to superior memory for emotional items), and against the possibility that responses in the emotional system at test are due to processing presented emotional stimuli rather than emotional memories, this new dataset eliminates any possibility that the post-sleep enhancements observed by Payne and Kensinger could have been associated with such confounding influences. Interestingly, Payne and Kensinger (2011) observed no increase in parahippocampal response, although they did observe heightened connectivity between parahippocampus/fusiform and other parts of the emotional memory system post-sleep. Because the parahippocampus mediates contextual associations (Bar et al., 2008), the marked heightening in response which we observed here may be task-specific.

4.3. Paradigm differences between Experiments 1 and 2

Experiments 1 and 2 differ not only in that Experiment 1 used overnight consolidation while Experiment 2 used daytime napping, but also in that the immediate test was performed only once, and without feedback, in Experiment 2, while it was performed twice with feedback in Experiment 1. The fact that Experiment 2 revealed a sleep-related reduction in context forgetting despite these differences shows that the initial finding could not have been associated with the repetitive encoding in Experiment 1. Interestingly, although the main effect of sleep was conserved across experiments, Experiment 2 showed a significant effect of encoding context valence during the immediate test which was not apparent in Experiment 1. This is likely associated with differences in encoding tasks as participants in Experiment 2 rated contextual stimuli for valence and arousal during training, leading to deeper encoding which likely impacted upon subsequent emotional memory.

4.4. Brain state during retention

Our observation of less context forgetting across a 12-h retention interval containing sleep than across an equivalent time period of daytime wakefulness (Fig. 2B) reinforces a growing literature suggesting that aspects of declarative memory are strengthened, or preferentially maintained, across sleep, see (Born, Rasch, & Gais, 2006; Walker, 2009) for reviews. Some authors speculate that elements of sleep physiology such as slow waves and sleep spindles may play an active role in consolidation (Born et al., 2006; Walker, 2009), while others maintain that the reduced forgetting observed across sleep is due to the relative absence of interfering stimuli see

(Ellenbogen et al., 2006) for both sides of the argument. Both possibilities are relevant to the current study, in which the Wake group spent the retention interval going about their normal daily activities, while the Sleep group obtained an average of 7.7 h of sleep in Experiment 1, and 1.5 h of sleep in Experiment 2. Although we cannot specifically determine the extent to which waking activities may have disrupted consolidation, previous work addressing this in skill learning (Huber et al., 2006; Mednick, Nakayama, & Stickgold, 2003; Walker, Brakefield, Morgan, Hobson, & Stickgold, 2002) and integration of declarative information (Cai, Mednick, Harrison, Kanady, & Mednick, 2009) describes performance deficits, rather than enhancements, when daytime activities are reduced or completely blocked to mimic the behavioural quiescence of sleep.

In addition to differences in activity levels, and in amounts of sleep obtained during the retention interval, the Sleep and Wake groups in Experiment 1 also differed in the diurnal time at which they performed the memory tasks. Specifically, the Sleep group was tested and scanned at approximately 9 AM, while the Wake group was tested and scanned at approximately 9 PM. This means that the results of Experiment 1 could potentially be due to circadian variations in physiology, rather than to sleep during the retention interval. We examined this possibility at the behavioural level by comparing performance on the immediate test (completed prior to consolidation) in the AM (Wake group) and the PM (Sleep group) and found no significant difference ($F = 0.334$, $p = 0.57$). Because the number of correctly attributed contexts was equivalent at these two times of day before consolidation (Fig. 2A), it is unlikely that the differential forgetting observed for Wake and Sleep groups was due to circadian influences on retrieval. Instead, such differences are more likely linked to differential consolidation during retention across these day or nighttimes intervals. To control for the possibility that such consolidation was associated with circadian characteristics of the retention period rather than with sleep itself, we repeated the behavioural component of this study using a napping paradigm in which all participants were trained at 11 AM and tested at 4 PM, but the Sleep group enjoyed a nap of approximately 90 min during the retention interval (see Fig. 2C and D). Our findings replicated the main-effect of sleep upon context memory as reported in the main study, Fig. 2B, and therefore reduce concern that this could have been due to circadian factors alone.

Turning to the functional data, our fMRI analysis was carefully designed to control for circadian effects where possible. We used a two tiered interaction in which items in the same experimental session were compared with each other prior to comparisons between Sleep and Wake groups. This meant that any responses associated with performing the task at a specific time of day were subtracted from the data ([context memory > correct rejections] for contrast 1 and [negative context memory > neutral context memory] for contrast 2) before Sleep and Wake groups were compared, ensuring that neural activities relating to the time of day were disambiguated from those relating to the difference between consolidation across sleep and wake. Furthermore, the interaction we observed between functional enhancement and task, whereby parts of the episodic memory system and amygdala were only activated in the Emotion task, but not in the People task (see Fig. 4), argues against a circadian explanation for our findings since diurnal effects would have to be task-specific in order to produce this pattern. Despite these efforts, we cannot completely rule out the possibility that a three way interaction between stimulus valence, retrieval task, and time of day may have contributed to the functional results. Future work should combine napping paradigms, sleep recording with polysomnography, and fMRI to verify that the observed alterations in brain activity are truly associated with sleep.

4.5. Summary

Overall, our data show that context memory decays less across an overnight retention interval containing sleep than across an equivalent interval of daytime wakefulness, and that this better memory for the context in which a stimulus was first seen is associated with stronger responses in the hippocampus and superior parietal cortex. Interestingly, the emotional content of contextual memories did not interact with this reduction in forgetting at the level of behavioural performance, suggesting that the selective impact of sleep upon memory for emotional information reported in prior studies (Hu et al., 2006; Nishida et al., 2009; Payne et al., 2008; Payne & Kensinger, 2011; Sterpenich et al., 2007, 2009; Wagner et al., 2005, 2006) may be limited to memory for the emotional image itself, or for detail within that image, and may not extend to the link between that image and associated information. Future work should establish the role of sleep physiology in the overnight protection of contextual memories and explicitly test for differences in how it impacts on emotional recognition and emotional context memory.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuropsychologia.2011.05.009.

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