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ORIGINAL ARTICLE

# Sleep's short-term memory preservation and long-term affect depotentiation effect in emotional memory consolidation: behavioral and EEG evidence

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## Abstract

**Study Objectives:** Sleep plays a pivotal role in the off-line processing of emotional memory. However, much remains unknown for its immediate vs. long-term influences. We employed behavioral and electrophysiological measures to investigate the short- and long-term impacts of sleep vs. sleep deprivation on emotional memory.

**Methods:** Fifty-nine participants incidentally learned 60 negative and 60 neutral pictures in the evening and were randomly assigned to either sleep or sleep deprivation conditions. We measured memory recognition and subjective affective ratings in 12- and 60-h post-encoding tests, with EEGs in the delayed test.

**Results:** In a 12-h post-encoding test, compared to sleep deprivation, sleep equally preserved both negative and neutral memory, and their affective tones. In the 60-h post-encoding test, negative and neutral memories declined significantly in the sleep group, with attenuated emotional responses to negative memories over time. Furthermore, two groups showed spatial-temporally distinguishable ERPs at the delayed test: while both groups showed the old-new frontal negativity (300–500 ms, FN400), sleep-deprived participants additionally showed an old-new parietal, Late Positive Component effect (600–1000 ms, LPC). Multivariate whole-brain ERPs analyses further suggested that sleep prioritized neural representation of emotion over memory processing, while they were less distinguishable in the sleep deprivation group.

**Conclusions:** These data suggested that sleep's impact on emotional memory and affective responses is time-dependent: sleep preserved memories and affective tones in the short term, while ameliorating affective tones in the long term. Univariate and multivariate EEG analyses revealed different neurocognitive processing of remote, emotional memories between sleep and sleep deprivation groups.

### Statement of Significance

It remains elusive regarding sleep's role in processing emotional memory, particularly how such impact unfolds over time. We documented that compared to sleep deprivation, sleep preserved the content of emotional memories and their affective tones in an immediate test, with declining memory and ameliorated negative affective tones in the longer term, that is, a short-term memory preservation and long-term affect depotentiation effect. Moreover, applying uni-/multi-variate EEG analyses to unravel the neural representation of emotion and memory processing revealed different neurocognitive processes underlying the recognition of remote memory in sleep and sleep deprivation groups. Our results shed light on how sleep impacts content and affective tones of emotional memories from dynamic time perspectives.

**Key words:** emotional memory; sleep deprivation; memory consolidation; ERP; short- vs. long-term effects

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## Introduction

Sleep and emotion are two well-established factors influencing how people remember and forget. Mounting evidence suggests that via off-line consolidation processes, sleep strengthens declarative memories and promotes episodic remembering of emotional experiences. However, much remains unclear regarding how sleep and emotion interact with each other in influencing memories and their affective tones. Specifically, three outstanding questions that await further investigations are: First, does sleep preferentially consolidate emotional over neutral memories? Second, does sleep preserve or attenuate the affective tones tagged to emotional memories? Third, will these impacts be long-lasting or only short-lived?

Emotion makes memories long-lasting. Existing research pinpoints the important roles of valence and arousal in the encoding of emotional memories [1]. However, beyond on-line encoding during wakefulness, whether preferential processing of emotional materials could continue during the off-line consolidation remains unclear. Earlier reports showed that compared to neutral or low-arousal materials, emotional or high-arousal materials are preferentially consolidated during sleep compared to an equal period of wakeful time. A nap shortly after encoding of emotional (vs. neutral) materials made emotional memories long-lasting even years later [2]. Intriguingly, sleep plays an active role in biasing the consolidation of different components from the same emotional scenes, such that the emotional components of the scenes (e.g. a burning car) were selectively preserved at the cost of peripheral, non-emotional elements (e.g. street or backyard; also known as emotional-memory trade-off effect) [3]. However, some studies failed to find a sleep-based emotion preferential effect; instead, they found that both sleep and wake equally consolidated emotional over non-emotional materials [4–8]. Two recent meta-analyses reported that while sleep does not selectively consolidate emotional memories over neutral memories, there are potential moderators (e.g. memory tests, whether sleep deprivation or daytime wakefulness as control conditions) that modulate such effects [9, 10].

In addition to memories, it remains contentious regarding how sleep modulates people's affective responses to emotional memories. Empirical findings are highly mixed: whilst some work suggested that sleep (vs. wakefulness) preserved emotional memories' affective tones as measured by both subjective ratings [5, 11–13] and physiological activities (e.g. heart rate deceleration [4]), other work found the opposite findings that sleep attenuated people's subjective or physiological activities to emotional memories [13–16]. While mixed results could be due to methodological differences (e.g. types of memory tests, measurements of affective responses, daytime vs. nighttime wakefulness, etc., for a review, see [17]), two theoretical accounts emerged accordingly: one proposes that sleep consolidates both emotional memory content and their associated affective tones [4, 5, 18]; alternatively, sleep preserves emotional memory content while attenuating affective responses [19, 20].

We consider time as an important factor in modulating sleep's impact on memory and affective tones. According to the Sleep to Forget and Sleep to Remember (SFSR) model, people's affective responses to emotional memories would decline across multiple nights of sleep (i.e. forget), while the content of the emotional memories is preserved (i.e. remembered) [19, 20]. Recent evidence provided support to this argument: Bolinger et al. [6] reported that compared to a wake group, sleep's beneficial effect on reducing affective responses only emerged after seven days. Therefore, it is important to consider time-dependent changes in assessing sleep's impact on emotional memories and their affective tones.

We aimed to test how sleep and sleep deprivation's impact on memory and affective responses unfold over time using immediate and delayed memory and affect rating tasks. We asked (1) whether sleep would preferentially consolidate negative over neutral memories; (2) how would sleep influence people's affective responses; (3) how would sleep's impacts on memory and affective responses change over time. During the delayed tests, we additionally recorded electroencephalograms (EEGs) to delineate retrieval processes supporting the recognition of remote memories. Specifically, we focused on two well-established, recognition-related event-related brain potentials (ERPs): an early 300–500 ms frontal negativity (FN400), and a late 600–1,000 ms parietal Late Positive Component (LPC). Regarding FN400, research suggests that old items would elicit smaller FN400s than novel items, particularly when people judge the items as "familiar" without remembering details from learning episodes. The LPC indicates vivid, conscious recollection, with larger amplitudes associated with more contextual details retrieved accompanying recognition [21, 22]. Given that sleep deprivation acutely disrupts sleep-dependent memory consolidation, we expected that participants from sleep and sleep deprivation groups would show different patterns of FN400 and LPC in the 60-h post-encoding test. Beyond a priori defined ERPs, we also applied multivariate ERP analyses (i.e. decoding and representational similarity analysis [RSA]) to study how sleep (vs. sleep deprivation) influences the neural representation of emotion (negative vs. neutral) and memory (old vs. new). Univariate and multivariate ERP analyses would provide complementary information elucidating the neurocognitive processes underlying recognition of remote emotional memory.

## Methods

### Participants

Sixty-two non-smoking healthy participants (42 females, with an average age of 20.48, *SD* = 2.03) were recruited from the University of Hong Kong via campus posters and mass email. Three participants were excluded for not completing the entire study, resulting in 59 participants (40 females, age 20.53 ± 2.06) in the final analyses. Participants gave their written consent forms before participation and were compensated with monetary incentives. The study was approved by the Human Research Ethics Committee of the University of Hong Kong.

Prior to lab visits, participants completed online prescreening for chronic medical conditions and current/history of diagnosed mental illnesses/neurological disorders/sleep disorders. They should have a regular sleep-wake pattern with averaged sleep time >6 h sleep time per night; not nauseous to blood, and no overnight shift work nor have intercontinental travels within the last two weeks or have such plans in the experimental week. Participants also completed four questionnaires as inclusion criteria: Insomnia Severity Index (ISI; ≤ 9) [23], Pittsburgh Sleep Quality Index (PSQI; ≤ 7) [24], Beck Depression Inventory-II (BDI-II; ≤11), [25] Depression, Anxiety and Stress Scale-21 (DASS-21; stress ≤ 14, anxiety ≤ 14, depression ≤ 12) [26].

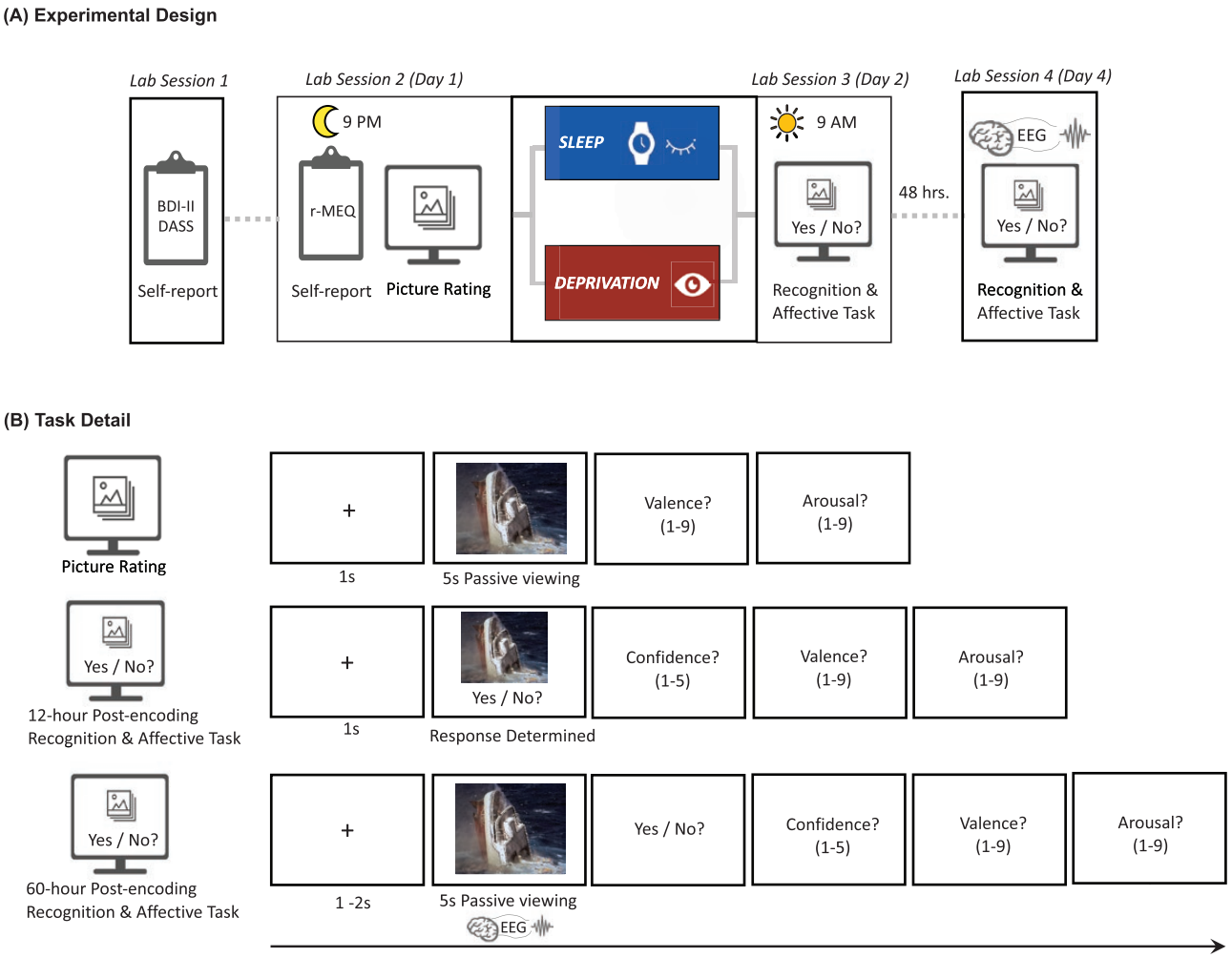


**Figure 1.** Experimental design and task details. (A) Participants incidental encoded the pictures while rating subjective affective experiences and then either go home to sleep or stay up overnight in the laboratory. In the next morning, participants completed the 12-h post-encoding recognition and affective ratings. After 48 h, participants came to the last session and completed 60-h post-encoding recognition and affective ratings, with their brain waves being recorded. (B) During the picture rating, each picture was presented for 5 s, followed by a 9-point scale rating for valence and arousal. For the testing phase, participants were tested on their memory with an old/new judgment, followed by a confidence and affective ratings. Pictures were selected from International Affective Picture System (IAPS) [27].

Participants who met the inclusion criteria were asked to maintain their usual sleep schedule, which was verified by pen-paper-based sleep diaries during the entire experiment period. Participants were asked to abstain from any caffeine and alcohol drinks 24 h before the experimental night (Day 1, see Figure 1, A).

## Materials

Stimuli consisted of 240 pictures (120 negative, 120 neutral) from the International Affective Picture System (IAPS) [27], which were divided equally into two sets (see Table 1 for IAPS normative ratings). These two stimuli sets were matched in the standardized valence and arousal ratings and were similar in semantic contents (objects, places, scenes). One set of stimuli was used in the incidental learning task (i.e. "old") on the first night of the experiment, before sleep and sleep deprivation manipulations. The other set of stimuli was used in the old/new recognition task as "new" stimuli. Because participants completed two recognition sessions, one 12-h post-encoding, the other one 60-h post-encoding, we used half of the old stimuli (30 negative and 30 neutral), together with half of the new stimuli (30 negative and 30 neutral), in each of the two recognition tasks. The two stimuli sets revealed no differences in terms of normative ratings (*p*s > 0.37, see Table 1) and were counterbalanced across participants.

**Table 1.** IAPS picture normative rating summary* (*N* = 240; mean ± *SD*)

| | Set A | Set B | Test |
|---|---|---|---|
| **Valence** | | | |
| Negative | 2.51 ± 0.63 | 2.49 ± 0.61 | $W = 1813$, $p = 0.95$ |
| Neutral | 5.04 ± 0.25 | 5.03 ± 0.26 | $W = 1827.5$, $p = 0.89$ |
| **Arousal** | | | |
| Negative | 5.96 ± 0.65 | 5.90 ± 0.63 | $t(118) = 0.55$, $p = 0.59$ |
| Neutral | 3.18 ± 0.54 | 3.11 ± 0.49 | $W = 1973$, $p = 0.37$ |

Note: * The ratings of chosen pictures were calculated from the normative ratings in the International Affective Picture System (IAPS) [27].

### Procedure

The whole study consists of four lab sessions spanning across at least seven days (see Figure 1, A). Participants first reported to the lab and were introduced to the entire experimental

procedure at least three days before the experimental night. They then completed BDI-II and DASS for the second time in the lab. Participants were given a sleep diary to keep records of their sleep patterns during the entire study period. A minimum of 3-day sleep record with normal sleep-wake patterns was required before they started the experimental night on Day 1.

On Day 1 experimental night, participants reported to the laboratory at around 9 pm. They completed the Reduced Morningness–Eveningness Questionnaire (r-MEQ) [28] to assess chronotype and rated their sleepiness level on the Stanford Sleepiness Scale (SSS) [29].

Participants then viewed 60 neutral and 60 negative pictures, and rated each picture along valence and arousal dimensions (Figure 1B). Each picture was presented for 5 s, followed by valence and arousal ratings on two 9-point Self-Assessment Manikin (SAM) scales (1 = negative/calm, 5 = neutral/normal, 9 = positive/arousal) [30]. Participants were instructed to pay full attention to pictures but were not given any instructions on upcoming memory tests (i.e. incidental encoding). They were then randomly assigned to either a sleep group or a total sleep deprivation group. Participants were only notified about their group assignments after the tasks to avoid any potential influence of group assignments on task performance.

Participants from the sleep group ($n$ = 29) were then instructed to go home and sleep as usual. Sleep durations were verified by self-report sleep diaries and by wrist actigraphy (Micro Motionlogger sleep watch, Ambulatory Monitoring Inc.). To match with the sleep deprivation group, participants were asked to refrain from consuming caffeine/alcohol, playing computer games, engaging in intense physical (e.g. running), or emotionally arousing activities (e.g. watching comedy or horror films) before the session in the next morning. They were required to come back to the laboratory the next morning, and light breakfasts were served.

Participants from the total sleep deprivation group ($n$ = 30) were instructed to stay in the lab with the company of two trained experimenters who took shifts during the night. During the overnight stay, participants' activities were kept at a minimum level of arousal: they were allowed to work on their assignments, read books, play board games, chat with the experimenters, take small walks, etc. They were required to refrain from watching videos, playing computer games, or engaging in intense physical or emotionally arousing activities. Non-caffeinated snacks were provided in the lab during the overnight stay, and light breakfasts were provided the next morning.

All participants started the Day 2 morning session (12-h post-encoding) around 9 am. They rated their sleepiness level through SSS and completed a recognition and affective rating task, in which they need to make old/new judgments with accuracy and speed equally emphasized, followed by confidence ratings on a scale of 1–5 (1 = not at all confident, 5 = highly confident), then valence and arousal rating using the SAM scale.

Thereafter, participants resumed their daily routine until Day 4 morning. They came back to the lab between 9 and 11 am, rated their sleepiness level, and completed a second, 60-h post-encoding recognition/affective rating task with high-density EEGs recorded. Each picture was presented for 5 s. to acquire EEG signals, followed by an old/new judgment, a confidence rating, and valence/arousal ratings (see Figure 1, B). Fixation cross presented for a jittered 1–2 s.

## Statistical analysis of behavior measure

Behavioral statistical analyses were performed using R version 3.6.0 [31]. For behavioral analyses, we excluded participants who failed to follow the instruction and whose scores fell beyond mean ±3 SDs among all participants collapsing across two groups. For EEG analyses, participants whose artifact trials exceeded 20% of total trials were excluded ($n$ = 0). The number of participants included in each analysis is presented in Table 2.

Performance from the old/new recognition task was analyzed based on the signal detection theory [32] and the EZ-diffusion model [33]. Specifically, we calculated the memory sensitivity $d'$ and response bias $C$ for each participant using the following formula: $d'$ = Z(hit rate) − Z(false alarm), $C$ = − (Z(hit rate) + Z(false alarm))/2, with hit rate referring to the proportion of "old" responses to old pictures and false alarm referring to the proportion of "old" responses to new pictures. Thus, a higher $d'$ indicates higher sensitivities in discriminating between old and new pictures, while a higher $C$ indicates a more stringent criterion in giving "old" responses (i.e. less likely to give an "old" response). We then conducted 2 (Group: sleep vs. sleep deprivation) × 2 (Time: 12- vs. 60-h post-encoding) × 2 (Emotion: negative vs. neutral) mixed ANOVA to $d'$ and $C$.

Because the short-term recognition test involved speeded binary forced-choice judgments, we applied an EZ-diffusion model to both RTs and accuracies to obtain the drift rate ($v$). A higher drift rate represents a faster information accumulation speed (see illustration in Figure 2, A). Consistent with a previous study [34], we excluded trials within each participant on which reaction time is beyond 3 median absolute deviation (MAD, 13.9% of trials were excluded). Drift rate was then analyzed through a 2 (Group: sleep vs. sleep deprivation) × 2 (Emotion: negative vs. neutral) mixed ANOVA.

Confidence ratings were analyzed using the mixed ordinal logistic regression model at a trial level with Group (sleep vs. sleep deprivation), Time (12- vs. 60-h post-encoding), Emotion (negative vs. neutral), and Memory (old vs. new) as model

**Table 2.** Number of participants included in different analysis (*N*)

| | Behavior Analyses* | | | | | EEG analyses† |
|---|---|---|---|---|---|---|
| | Sensitivity ($d'$) | Response bias ($C$) | Drift rate ($v$) | ΔValence | ΔArousal | ERP |
| **Sleep** | 29 | 29 | 29 | 29 | 24 | 27 |
| **Sleep Deprivation** | 28 | 30 | 30 | 28 | 28 | 30 |
| **Total (*N*)** | 57 | 59 | 59 | 57 | 52 | 57 |

Note: * Behavior analyses excluded participants who failed to follow instructions and whose scores fall beyond ±3 SDs across the two groups.
†Two participants only finished behavioral task with no EEGs recording.

predictors, while participants and individual pictures were entered as random intercepts to control individual differences and idiosyncratic features of each picture (see Supplement Result S1).

To analyze the changes of affective ratings, we focused on old pictures and calculated change scores Δvalence and Δarousal, with short-/long-term test ratings minus baseline ratings (from Day 1) of the same item. A positive (negative) Δvalence thus indicates more positive (negative) ratings compared to its baseline, while a positive (negative) Δarousal indicates higher (lower) arousal ratings compared to its baseline. Both Δvalence and Δarousal were then analyzed through 2 (Group: sleep vs. sleep deprivation) × 2 (Time: 12- vs. 60-h post-encoding) × 2 (Emotion: negative vs. neutral) mixed ANOVA.[1] To examine how sleep and sleep deprivation impact participants' affect responses to novel affective pictures at different time points, we analyzed these affective ratings using baseline rating as covariate (see Result S2.).

## Electrophysiological recording and preprocessing

During the 60-h post-encoding test session, EEGs were recorded using a 64-channel cap (eego mylab, ANT Neuro, Germany) with electrodes positioned according to the 10–5 International System with one additional electrooculogram (EOG) channel. Continuous EEGs were recorded with an online sampling rate of 500 Hz with reference at CPz. Impedance was kept below 20 kΩ during recording.

For off-line analyses, continuous EEGs were preprocessed using EEGLAB [35] and ERPLAB [36] toolbox in MATLAB (The Mathworks, Natick, MA). Data were first down-sampled to 250 Hz and band-passed between 0.1 and 30 Hz. A 50 Hz notch filter was applied to remove AC interference. All data were re-referenced to the common average. For ERP analyses, continuous EEGs were segmented into –200–1,000 ms epochs relative to the onset of pictures. ERPs were baseline corrected using the averaged amplitude of the 200 ms pre-stimulus segments. Independent component analyses (ICA) were used to remove eye blinks and muscle movements. Artifacts were marked and rejected using 200 ms moving windows with a 100-ms step size when peak-to-peak amplitude exceeded ±100 microvolts.

[1] Adding coffee/alcohol consumption or recovery sleep duration as covariates did not influence our results. None of the covariates were significant. See detailed results in Supplement Result S4.

## Univariate ERP analyses

For ERP analyses, we only included trials with correct responses: hit (HT, i.e. correctly recognized old pictures) and correct rejection (CR, i.e. correctly rejected new pictures) trials. Out of 60 trials containing old pictures and 60 trials containing new pictures, the sleep group had 46.44 ± 9.70 HT trials and 53.67 ± 4.88 CR trials, while the sleep deprivation group had 46.03 ± 11.06 HT trials and 53.27 ± 3.93 CR trials (see details in Table 3). No significant group differences in the number of trials were found (*p*s > 0.74). ERPs were then averaged within each of the four conditions: negative_HT, negative_CR, neutral_HT, neutral_CR. Given our interests in memory-related processes (see Figure 1, B), we measured the following recognition-related ERP components: mean amplitudes of 300-500ms FN400 collapsing across frontocentral electrodes FCz, FC1/2, Cz, C1/2; and of 600–1,000 ms LPC collapsing across centroparietal electrodes CP1/2, Pz, P1/2 [21, 22, 37]. For statistical testing, we conducted 2 (Group: sleep vs. sleep deprivation) × 2 (Emotion: negative vs. neutral) × 2 (Memory: HT vs. CR) mixed ANOVAs on ERP amplitudes.

## Multivariate analyses

*Multivariate pattern classification (decoding)*. To unravel the time course of image processing, we conducted decoding analyses

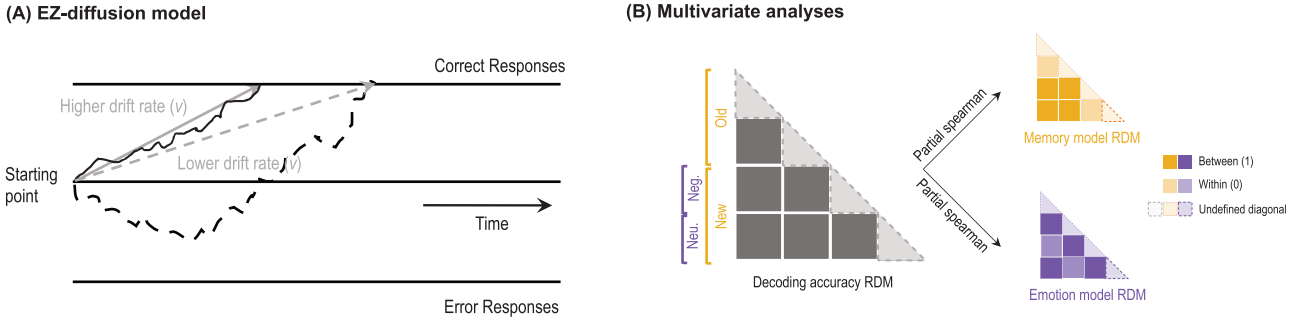


**Figure 2.** Model illustration. (A) EZ-diffusion model. The model considers the process of making a decision is a process of information accumulation. The starting point of such process is assumed to be the middle point between the upper and lower boundaries. When information is accumulated enough to across either boundary, decision will be made. A higher drift rate describes a higher information accumulation speed (gray solid line), lower drift rate describes a slower accumulation rate (gray dashed line). (B) Multivariate analyses. To dissociate different effects, we constructed model representational dissimilarity matrix (RDM) for memory (orange, old vs. new) and emotion (purple, negative vs. neutral; 1 represent between category and 0 represents within category). We computed partial spearman correlation between each model RDM and decoding RDM at every time point for each participant, while partialing out the alternative model.

**Table 3.** Trial number included in the univariate ERP analysis (mean ± *SD*)

| | Sleep (*N* = 27) | Deprivation (*N* = 30) | | Sleep (*N* = 27) | Deprivation (*N* = 30) |
|---|---|---|---|---|---|
| **Hit trials** | | | **Correct rejection trials** | | |
| Negative | 23.78 ± 5.08 | 23.73 ± 5.64 | Negative | 26.41± 2.87 | 27.00 ± 1.88 |
| Neutral | 22.67 ± 5.00 | 22.3 ± 5.91 | Neutral | 27.26 ± 2.35 | 26.27± 2.9 |

based on the spatial distribution of the averaged ERPs in sleep and sleep deprivation groups. MATLAB scripts for decoding were adapted from [38]. Specifically, based on the preprocessed ERPs from 61 electrodes, we used a binary support vector machine (SVM) classifier to decode between every two conditions (in total, six comparisons resulted from four conditions: old/negative, old/neutral, new/negative, and new/neutral) at each time point from –200 to 1,000 ms time window. We used a 5-fold cross-validation procedure: for each participant and each condition, 30 trials (if none was rejected) from each condition were divided into five sets, with each set containing six epochs. Data were then averaged within each set and resulted in five sub-ERPs for each condition. Four of the five averaged sub-ERPs were used as a training set, and then the performance was tested with the fifth sub-ERPs. This procedure was repeated five times, with each of the five sets being testing data and the rest four being training data. To achieve robust decoding, this procedure was repeated 10 times with different random assignments to generate the five averaged sub-ERPs. Decoding accuracy was calculated by comparing the true condition label with the predicted label and averaged over iterations. Results of decoding accuracy for each pairwise comparison are presented in Supplement Result S3.

The decoding procedure was performed for 6 pairwise comparisons (i.e. [4 conditions × 3]/2 = 6 combinations), resulting in a 4 × 4 decoding representational dissimilarity matrix (RDM; see Figure 2, B for illustration) for each participant and time point. This decoding RDM is symmetric and undefined at the diagonal, which would be applied to later representational similarity analysis.

*Representational similarity analysis (RSA)*. To disentangle different neural representations of emotion and memory, we refer to the methods used in [39] and further applied representational similarity analysis (RSA) by constructing model representational dissimilarity matrix (RDM) for emotion and memory separately (see Figure 2, B). The model RDMs were 4 × 4 binary matrices with 1 corresponds to between condition (e.g. negative vs. neutral, dissimilarity = 1) and 0 corresponds to within conditions (e.g. negative vs. negative, dissimilarity = 0). The lower-diagonal matrices were extracted and correlated with the decoding RDMs using partial Spearman correlation for each participant and time point. The partial Spearman correlation allows partialing out the influence of the alternative model: correlating decoding RDM with memory model RDM while controlling for emotion model RDM, and vice versa. A higher positive correlation coefficient thus represents a stronger neural representation of emotion/memory that can be decoded from the whole-brain EEGs. Each participant's correlation coefficient at each time point was then Fisher Z-transformed to adjust for non-normality.

*Statistical inference*. To control for false positives due to multiple comparisons, we performed non-parametric statistical tests on decoding accuracy (see Supplement S3) and partial correlation coefficients. We employed a nonparametric cluster-based Monte Carlo simulation technique [38]. The null hypotheses were that the decoding accuracy was at chance level (i.e. 1/2, see Supplement S3) and that the correlation coefficients/differences were 0. Note that when comparing decoding accuracies against chance level and comparing correlation coefficient to 0, we used one-tailed tests given that the SVM decoding analyses yield no meaningful below-chance results [38] and that the correlation with the model RDM was only meaningful for positive values [39].

To construct null distributions, we first shuffled the true condition labels of the ERP data. For this permutated dataset, we further identify the maximum sum of test statistics (i.e. maximum *t*-mass) of the consecutive significant time points. This procedure was repeated 10,000 times, resulting in a permutation null distribution with 10,000 summed-t values. Then we compared the observed cluster-level *t*-mass with the null distribution, and conclude that any observed cluster-level *t*-mass that fell in the 95% percentile of the null distribution counts as significant time points (exception: when comparing within-group correlation differences, *t*-mass fell beyond 2.5% and 97.5% counts as significance [two-tailed]).

To test the significance of between-group differences, we constructed the null distribution by randomly shuffling the group label of the single-participant decoding accuracy. Observed cluster-level *t*-mass was based on two-tailed independent *t*-tests. Significance was reported if the observed *t*-mass fell beyond 2.5% and 97.5% of the constructed null distribution.

## Results

Demographic information is presented in Table 4. No significant baseline differences were found between groups. Actigraphy-based sleep parameters obtained from the sleep group are presented in Table 5. Overall, participants in the sleep group slept for 6.76 ± 0.89 h (actigraphy-based) and they reported that they slept for 7.5 ± 1.01 h (dairy-based) in the experimental night.

Sleepiness was assessed on Day 1 night, Day 2 morning and Day 4 EEG session. A mixed Group × Time ANOVA revealed a significant Group × Time interaction ($F(2,110) = 56.36$, $p < 0.001$, $\eta_p^2 = 0.51$). Further analyses showed no group differences on sleepiness on Day 1 night (i.e. initial encoding), sleep: 3.07 ± 1.15 vs. sleep deprivation: 2.62 ± 0.82; $t(134.09) = 1.61$, $p = 0.11$; but a significant group difference on Day 2 morning due to sleep vs. sleep deprivation manipulations (2.07 ± 1.18 vs. 4.83 ± 1.34; $t(134.09) = -9.83$, $p < 0.001$). On Day 4 EEG session, both groups reported comparable sleepiness level (sleep: 2.39 ± 0.74 vs. sleep deprivation: 2.52 ± 0.99; $t(134.09) = -0.44$, $p = 0.66$).

### Memory performance

Hit rate, false alarm rate, *d'* and *C* are summarized in Table 6.

*Memory sensitivity (d')*. The 2 (Group) × 2 (Emotion) × 2 (Time) ANOVAs revealed a significant main effect of Group, $F(1,55) = 4.16$, $p = 0.046$, $\eta_p^2 = 0.07$, suggesting slept participants showed higher memory sensitivities than the sleep-deprived participants (2.95 ± 0.93 vs. 2.61 ± 0.83, Cohen's $d = 0.54$). We also found a significant main effect of Time, as memory declined from 12-h to 60-h post-encoding ($F(1,55) = 53.01$, $p < 0.001$, $\eta_p^2 = 0.49$). The main effect of emotion was not significant ($F(1,55) = 2.19$, $p = 0.145$, $\eta_p^2 = 0.038$). Importantly, we found a significant Group × Time interaction ($F(1,55) = 8.30$, $p = 0.006$, $\eta_p^2 = 0.13$). Thus, slept participants were more accurate than their sleep-deprived counterparts in recognizing both negative and neutral pictures in the 12-h post-encoding test ($t(79.3) = 3.09$, $p = 0.003$), but there were no group differences in the 60-h post-encoding test ($t(79.3) = 0.58$, $p = 0.56$). The Group × Emotion interaction was not significant: $F(1,55) = 0.12$, $p = 0.730$, $\eta_p^2 = 0.002$.

Critically, we observed a significant Group × Time × Emotion three-way interaction ($F(1,55) = 5.37$, $p = 0.024$, $\eta_p^2 = 0.089$; see

**Table 4.** Demographic information for sleep and sleep deprivation group ($N$ = 59; mean ± $SD$)

| | Sleep ($N$ = 29) | Sleep deprivation ($N$ = 30) | Test statistics & $p$ value |
|---|---|---|---|
| **Age** | 20.62 ± 2.48 | 20.43 ± 1.59 | $W$ = 408.50; $p$ = 0.69 |
| **Gender** | | | |
| Male, $n$ (%) | 7 (24.14%) | 12 (40.00%) | |
| Female, $n$ (%) | 22 (75.86%) | 18 (60.00%) | $\chi^2(1)$ = 1.70; $p$ = 0.19 |
| **Insomnia Severity Index (ISI)** | 3.52 ± 1.99 | 4.30 ± 2.45 | $t(57)$ = –1.34; $p$ = 0.18 |
| **Pittsburgh Sleep Quality Index (PSQI)** | 3.45 ± 1.40 | 4.00 ± 1.49 | $W$ = 350; $p$ = 0.19 |
| **(Online) Beck Depression Inventory-II (BDI-II)** | 3.55 ± 3.16 | 4.20 ± 3.73 | $W$ = 403; $p$ = 0.63 |
| **(Online) Depression Anxiety Stress Scales (DASS)** | | | |
| Depression | 2.69 ± 3.39 | 1.87 ± 2.29 | $W$ = 391; $p$ = 0.48 |
| Anxiety | 3.52 ± 3.05 | 3.80 ± 3.61 | $W$ = 431; $p$ = 0.96 |
| Stress | 2.90 ± 3.61 | 4.27 ± 3.73 | $W$ = 330; $p$ = 0.10 |
| **(In-lab) Beck Depression Inventory-II (BDI-II)** | 3.72 ± 3.68 | 4.27 ± 3.31 | $W$ = 381; $p$ = 0.41 |
| **(In-lab) Depression Anxiety Stress Scales (DASS)** | | | |
| Depression | 2.14 ± 2.92 | 2.87 ± 3.00 | $W$ = 354.50; $p$ = 0.20 |
| Anxiety | 4.21 ± 3.56 | 4.27 ± 3.55 | $W$ = 428.00; $p$ = 0.92 |
| Stress | 3.24 ± 3.56 | 4.40 ± 4.34 | $W$ = 367.50; $p$ = 0.30 |
| **Morningness-Eveningness Questionnaire (MEQ)** | | | |
| Morningness type | 4 (13.79%) | 1 (3.33%) | |
| Eveningness type | 7 (24.14%) | 7 (23.33%) | |
| Neither type | 18 (62.07%) | 22 (73.33%) | $\chi^2$ = 2.18; $p$ = 0.37 |
| **Sleep duration (the night before experiment)** | | | |
| Sleep diary | 8.21 ± 1.16 | 8.15 ± 0.97 | $W$ = 388; $p$ = 0.96 |

Note: To compare between group differences, for continuous data, independent sample t-tests ($t$) were conducted if assumption was met. Otherwise, Wilcoxon rank-sum tests ($W$) would be performed instead. For count data, chi-sqaure test ($\chi^2$) was conducted. *$p$ < 0.05; **$p$ < 0.01.

**Table 5.** Data summary obtained from actigraphy in sleep group ($N$ = 28)

| | Sleep ($N$ = 28) |
|---|---|
| **Averaged bed time** | 00:25 am |
| **Averaged wake time** | 07:47 am |
| **Duration in bed (min)** | |
| Mean ± $SD$ | 443.18 ± 60.44 |
| Range | [270, 611] |
| **Sleep time (min)** | |
| Mean ± $SD$ | 405.71 ± 53.44 |
| Range | [232†, 492] |
| **Sleep latency (min)** | |
| Mean ± $SD$ | 22.54 ± 38 |
| Range | [3, 168] |
| **Sleep efficiency (in %)** | |
| Mean ± $SD$ | 96.68 ± 3.72 |
| Range | [87.44, 100] |
| **Wake after sleep onset** | |
| Mean ± SD | 14.11 ± 16.15 |
| Range | [0, 53] |

Note: *One participant failed to follow the instruction of using the actigraphy and thus was excluded from the summary.
†Note that there was one participant who slept for 232 min. Based on our criteria in excluding data (i.e. beyond ±3SDs for behavioral analyses/have >20% artefact trials for EEG analyses), this participant was included in all analyses, except for Δarousal, wherein the performance of this participant was excluded as an outlier.

Figure 3, A). Following up the significant three-way interaction, we examined memory changes by conducting 2 (Emotion) × 2 (Time) ANOVAs within each group respectively. In the sleep group, we only found a significant Time effect, as both negative and neutral memories declined significantly from 12- to 60-h post-encoding ($F(1,28)$ = 81.58, $p$ < 0.001, $\eta_p^2$ = 0.74). In the sleep deprivation group, however, we found a significant Emotion × Time interaction ($F(1,27)$ = 6.30, $p$ = 0.018, $\eta_p^2$ = 0.19). This interaction was driven by a significant decline of neutral memories (12- vs. 60-h, $t(49.5)$ = 3.61, $p$ < 0.001) while negative memories remained unchanged ($t(49.5)$ = 0.64, $p$ = 0.52). Furthermore, sleep-deprived participants showed numerically higher sensitivities for negative than for neutral memories in the delayed test but did not reach statistical significance ($t(45.2)$ = 1.95, $p$ = 0.058; see EEG evidence in Supplement Figure S2, B). These results suggested that while both negative and neutral memories significantly declined to a similar extent in the sleep group, sleep-deprived participants showed preservation of negative relative to neutral memories over time.

Overall, *d'* analyses suggested a time-dependent role of sleep in consolidating emotional memories, as evidenced by an immediate preservation effect followed by a significant time decline.

*Response bias (C)*. The same three-way ANOVA for response bias revealed a significant main effect of Emotion: $F(1,57)$ = 5.26, $p$ = 0.025, $\eta_p^2$ = 0.085: overall, participants were more likely to judge negative pictures as "old" than neutral pictures, that is, a more liberal response bias. Moreover, the effect of Time is significant: $F(1,57)$ = 46.14, $p$ < 0.001, $\eta_p^2$ = 0.45, as participants became more conservative over time. Importantly, we found a significant Emotion × Group interaction (see Figure 3, B; $F(1,57)$ = 4.47, $p$ = 0.039, $\eta_p^2$ = 0.073): slept participants showed more liberal response biases in judging negative than neutral pictures ($t(57)$ = –3.09, $p$ = 0.003); while sleep-deprived participants showed similar response biases in judging negative and neutral pictures ($t(57)$ = –0.13, $p$ = 0.898, see Figure 3, B). No other significant effects were found ($ps$ > 0.208).

*Drift rate (v)*. The two-way ANOVA showed an absence of Group × Emotion interaction (see Figure 3, C; $F(1,57)$ = 0.027, $p$ = 0.87, $\eta_p^2$ = 0.00) but an insignificant trend in Group effect ($F(1,57)$ = 2.74, $p$ = 0.10, $\eta_p^2$= 0.046) with a moderate effect size (Cohen's $d$ = 0.43).

**Table 6.** Summary for memory performance (*N* = 59; mean ± *SE*)

| | Sleep (*N* = 29) | Deprivation (*N* = 30) | | Sleep (*N* = 29) | Deprivation (*N* = 30) |
|---|---|---|---|---|---|
| **Hit rate*** | | | **False alarm†** | | |
| **Lab session 3** | | | **Lab session 3** | | |
| Negative | 0.94 ± 0.02 | 0.88 ± 0.03 | Negative | 0.08 ± 0.01 | 0.13 ± 0.02 |
| Neutral | 0.93 ± 0.01 | 0.89 ± 0.03 | Neutral | 0.09 ± 0.01 | 0.12 ± 0.02 |
| **Lab session 4** | | | **Lab session 4** | | |
| Negative | 0.81 ± 0.03 | 0.80 ± 0.03 | Negative | 0.10 ± 0.02 | 0.08 ± 0.01 |
| Neutral | 0.77 ± 0.03 | 0.76 ± 0.03 | Neutral | 0.08 ± 0.01 | 0.11 ± 0.02 |
| | Sleep (*N* = 29) | Deprivation‖ (*N* = 28) | | Sleep (N = 30) | Deprivation (N = 30) |
| **Memory sensitivity (*d'*)‡** | | | **Memory bias (C)§** | | |
| **Lab session 3** | | | **Lab session 3** | | |
| Negative | 3.47 ± 0.16 | 2.72 ± 0.18 | Negative | –0.16 ± 0.08 | –0.05 ± 0.07 |
| Neutral | 3.24 ± 0.16 | 2.85 ± 0.16 | Neutral | –0.07 ± 0.07 | –0.05 ± 0.08 |
| **Lab session 4** | | | **Lab session 4** | | |
| Negative | 2.61 ± 0.16 | 2.61 ± 0.15 | Negative | 0.14 ± 0.11 | 0.28 ± 0.10 |
| Neutral | 2.47 ± 0.14 | 2.25 ± 0.12 | Neutral | 0.37 ± 0.09 | 0.29 ± 0.09 |

Note: * Hit rate: the number of old pictures that were correctly recognized divided by total number of old pictures.
† False alarm: the number of new pictures that were wrongly recognized as old divided by total number of new pictures.
‡Sensitivity (*d'*): the standard scores of hit rate minus the standard scores of false alarm.
§ Response bias (*C*): the reverse of the average of the standard scores of hit rate and false alarm.
‖ In *d'* analysis, two participants from sleep deprivation group were excluded from analysis for their scores fell beyond ± 3*SD*s.

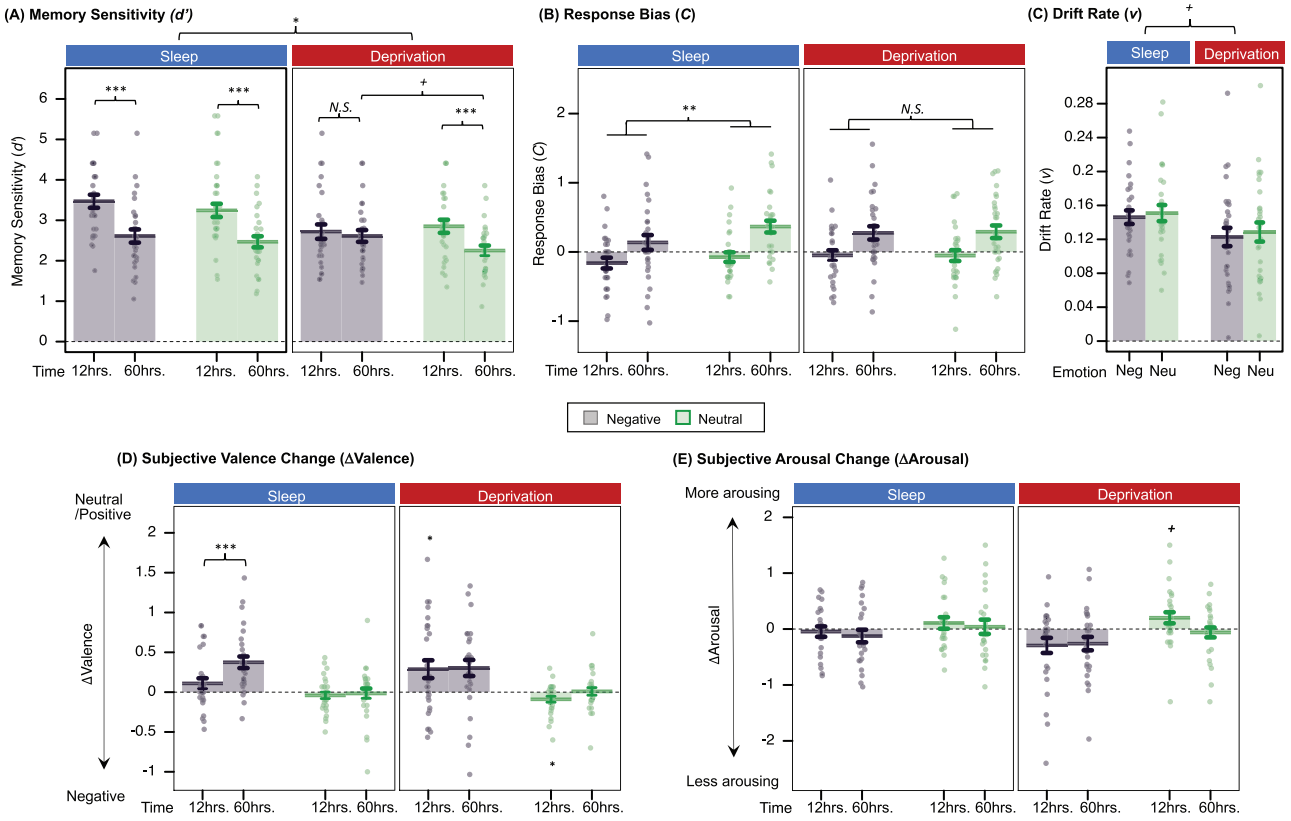


**Figure 3.** Behavior results. (A) Memory sensitivity (*d'*) across group, time and emotion. Sleep group showed decline in both negative and neutral memories over time, while sleep deprivation group exhibited decline only in neutral memories. Negative memories in sleep deprivation group were selectively preserved. (B) Response Bias (*C*) across group, time and emotion. In sleep group, negative memories were less biased than neutral memories. No emotion differences found in sleep deprivation group. (C) Drift rate (*v*) across group and emotion. No Group × Emotion interaction was found. Sleep group had a marginally higher information accumulation speed than sleep deprivation group. (D) Group × Emotion × Time on Valence Change (Δvalence). Sleep group rated negative pictures more neutrally over time. Sleep deprivation group showed an impairment in emotional evaluation in 12-h immediate test. (E) Group × Emotion × Time on Arousal Change (Δarousal). No group-related effects were found. Error bar represents ±1 *SEM*. ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$; ⁺$p < 0.1$; N.S. non-significant.

A higher drift rate suggested that slept participants were numerically faster in information accumulation than sleep-deprived participants. Thus, slept participants were not only more accurate in discriminating between old and new pictures (i.e. *d'*), they also achieved decisions more efficiently than sleep-deprived participants (i.e. *v*; note the trend was not statistically significant), both of which exhibited an emotion-independent pattern.

### Affective rating changes

*ΔValence*. The omnibus Group × Emotion × Time ANOVA revealed a significant main effects of Emotion: $F(1,55) = 28.48$, $p < 0.001$, $\eta_p^2 = 0.34$, such that ratings toward negative pictures became more positive (vs. baseline, i.e. larger Δvalence) than neutral pictures. We also found a significant main effect of Time: $F(1,55) = 5.68$, $p = 0.021$, $\eta_p^2 = 0.094$, such that participants rated pictures more positively (i.e. larger Δvalence) from 12- to 60-h post-encoding. Importantly, we found a significant Group × Time × Emotion three-way interaction ($F(1,55) = 4.31$, $p = 0.043$, $\eta_p^2 = 0.073$; see Figure 3, D). Following up the interaction, we examined Δvalence by conducting 2 (Emotion) × 2 (Time) ANOVAs in sleep and sleep deprivation group, respectively. In the sleep group, we found a significant two-way interaction ($F(1,28) = 7.06$, $p = 0.013$, $\eta_p^2 = 0.20$): ratings toward negative pictures became more positive (i.e. larger Δvalence) in the 60-h than the 12-h post-encoding test ($t(54.5) = -3.77$, $p < 0.001$); while no time-related changes were found in neutral pictures ($t(54.5) = -0.34$, $p = 0.73$). In the sleep deprivation group, we did not find any time-related effect (*p*s > 0.39). We also examined the Group × Emotion interactions in the 12- and 60-h post-encoding tests, to understand how sleep and sleep deprivation differentially impact Δvalence at different time points. The interaction effect in both the 12- and 60-h post-encoding test failed to reach significance, $F(1,55) = 2.95$, $p = 0.091$, $\eta_p^2 = 0.051$; $F(1,55) = 0.46$, $p = 0.501$, $\eta_p^2 = 0.008$.

In the 12-h post-encoding test, we further visually inspected the Emotion effect within the sleep deprivation group and found an interesting pattern: sleep-deprived participants rated negative pictures more positively (Δvalence > 0) and neutral pictures more negatively (Δvalence < 0) in the 12-h post-encoding test (see Figure 3, D). Thus, we conducted an exploratory analysis using two-tailed one-sample *t*-tests (Δvalence vs. 0) for negative and neutral pictures, separately. Results showed that sleep-deprived participants rated negative memories more positively (Δvalence > 0, $t(27) = 2.57$, $p = 0.016$), and they rated neutral memories more negatively (Δvalence < 0, $t(27) = -2.42$, $p = 0.023$). Note that this pattern was not observed in sleep group: negative picture: $W = 178$, $p = 0.23$; neutral picture: $t(28) = -1.00$, $p = 0.33$. These results suggested that sleep-deprived participants, but not slept participants, became less sensitive in distinguishing valences between negative and neutral memories.

*ΔArousal*. The omnibus ANOVA on Δarousal revealed no Group-related significant effects (*p*s > 0.116, see Figure 3, E). However, visual inspection of the data in the sleep deprivation group suggests a similar pattern as in Δvalence but did not reach statistical significance: immediately after sleep deprivation, sleep-deprived participants rated negative pictures as less arousing (i.e. Δarousal < 0, $W = 116$, $p = 0.13$) but neutral pictures as more arousing (i.e. Δarousal > 0, two-tailed one-sample *t*-test, $t(27) = 2.03$, $p = 0.052$). However, slept participants did not show arousal rating changes (negative: $t(23) = -0.5$, $p = 0.63$; neutral: $t(23) = 1.05$, $p = 0.30$).

### Univariate ERP analyses

Grand-averaged ERPs of different electrode clusters are presented in Figure 4.

*FN400:* The mixed 2 (Group: sleep vs. sleep deprivation) × 2 (Emotion: negative vs. neutral) × 2 (Memory: HT vs. CR) three-way ANOVA revealed significant main effects of Memory ($F(1,55) = 6.55$, $p = 0.013$, $\eta_p^2 = 0.11$) and Emotion ($F(1,55) = 42.25$, $p < 0.001$, $\eta_p^2 = 0.44$): both groups exhibited a more negative FN400 in CR vs. HT, and in negative vs. neutral pictures. We also observed a significant Emotion × Memory interaction ($F(1,55) = 5.21$, $p = 0.026$, $\eta_p^2 = 0.086$; see Figure 4, A). Pair-wise comparison showed that for neutral pictures, CR stimuli elicited more negative-going FN400 than HT stimuli ($t(110) = -3.42$, $p < 0.001$), while for negative pictures, CR and HT stimuli elicited comparable FN400 responses ($t(110) = 0.20$, $p = 0.84$; discussion see Supplement Discussion S1).

*LPC*. We found a significant main effect of Memory ($F(1,55) = 8.41$, $p = 0.005$, $\eta_p^2 = 0.13$) and Emotion ($F(1,55) = 14.95$, $p < 0.001$, $\eta_p^2 = 0.21$), with larger LPCs for HT vs. CR and for negative vs. neutral pictures. Importantly, we found a significant Group × Memory interaction ($F(1,55) = 6.35$, $p = 0.015$, $\eta_p^2 = 0.10$). Planned comparisons suggested that sleep-deprived participants showed larger LPCs for HT vs. CR pictures ($t(55) = 3.94$, $p < 0.001$), while slept participants showed no such difference ($t(55) = 0.26$, $p = 0.79$).

### Multivariate analyses

The time-resolved decoding accuracy of the six pairwise comparisons can be found in Supplement Result S3.

Neural representations revealed by RSA suggested that in both sleep and sleep deprivation groups, whole-brain ERPs would represent emotion but not memory (see Figure 5). The neural representations of emotion were more robust in sleep group (during 340–840 ms, $p < 0.001$) than in sleep deprivation group (two discrete clusters, 360–460 ms, $p = 0.037$, 780–920 ms, $p = 0.028$), although between-group differences did not reach statistical significance.

When comparing the emotion vs. memory neural representations within each group, we observed an enhanced emotion (vs. memory) representation only in the sleep group (one cluster, 340–800 ms, $p < 0.001$). In contrast, the sleep deprivation group showed enhanced memory (vs. emotion) representation in an early time window (20–120 ms, $p = 0.045$). These results suggested that sleep and sleep deprivation led to differential neural representations for emotion and memory even after 48 h.

## Discussion

A night of sleep (vs. sleep deprivation) equally preserved negative and neutral memories in the post-encoding 12-h test, followed by a significant decline from 12- to 60-h post-encoding test (i.e. a short-term memory preservation effect). Results from affective ratings suggested a long-term affect depotentiation effect of sleep: there was initial preservation of affective tones in a 12-h post-encoding test but attenuated negative ratings over time. Interestingly, the sleep deprivation group selectively preserved negative memories over time, while neutral memories significantly declined. Event-related potentials (ERPs) analyses during the delayed test revealed that while both groups showed the frontal FN400 old-new effect, only the

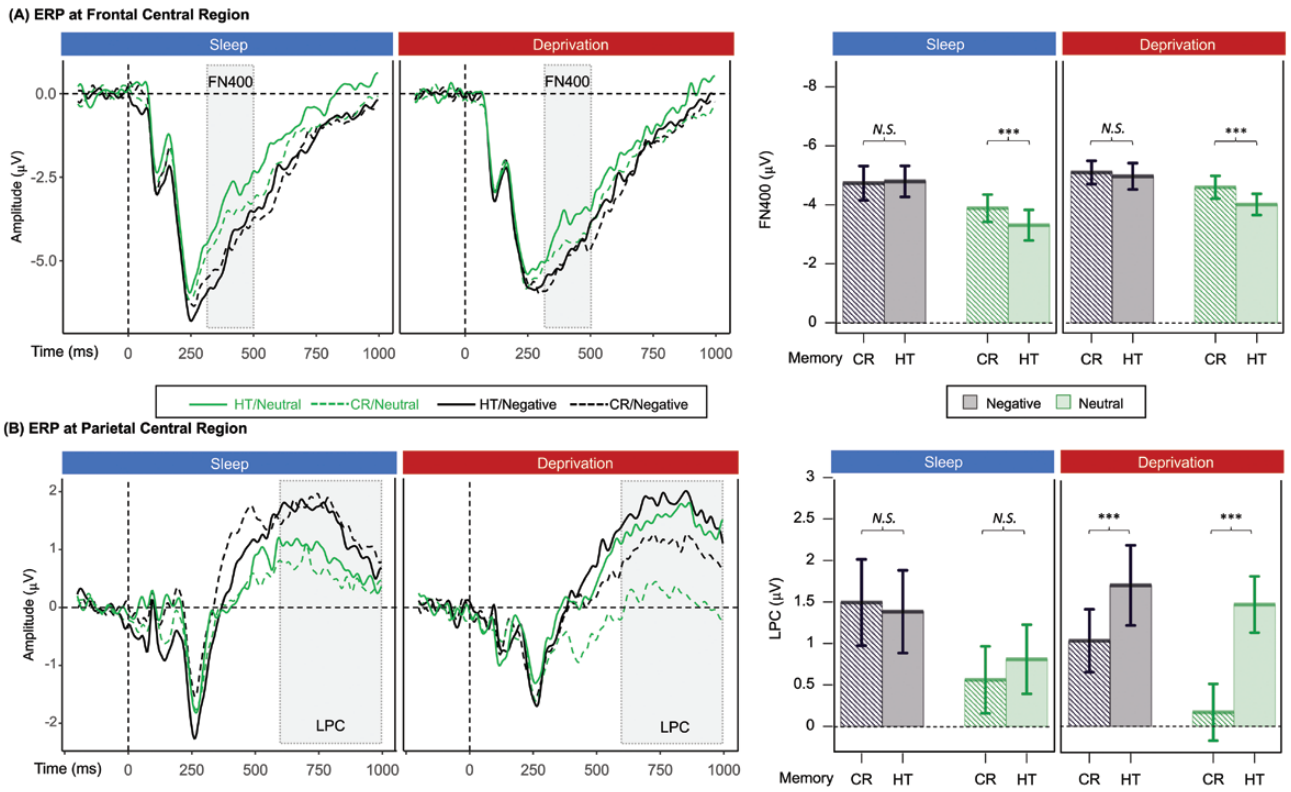


**Figure 4.** ERP results. (A) ERP results at frontal central region and associated ANOVA results. Memory × Emotion was significant, suggesting participants showed a more negative going FN400 on correct rejected trials than hit trials only when judging neutral pictures, but not negative pictures. Main effects of Memory and Emotion were significant. (B) ERP at parietal central region and associated ANOVA results. We found a significant Group × Memory effect, with sleep deprivation group exhibited larger old-new effect than sleep group. Error bar represents ±1 SEM. CR: correct rejection; HT: hit; ***$p < 0.001$; N.S., non-significant.

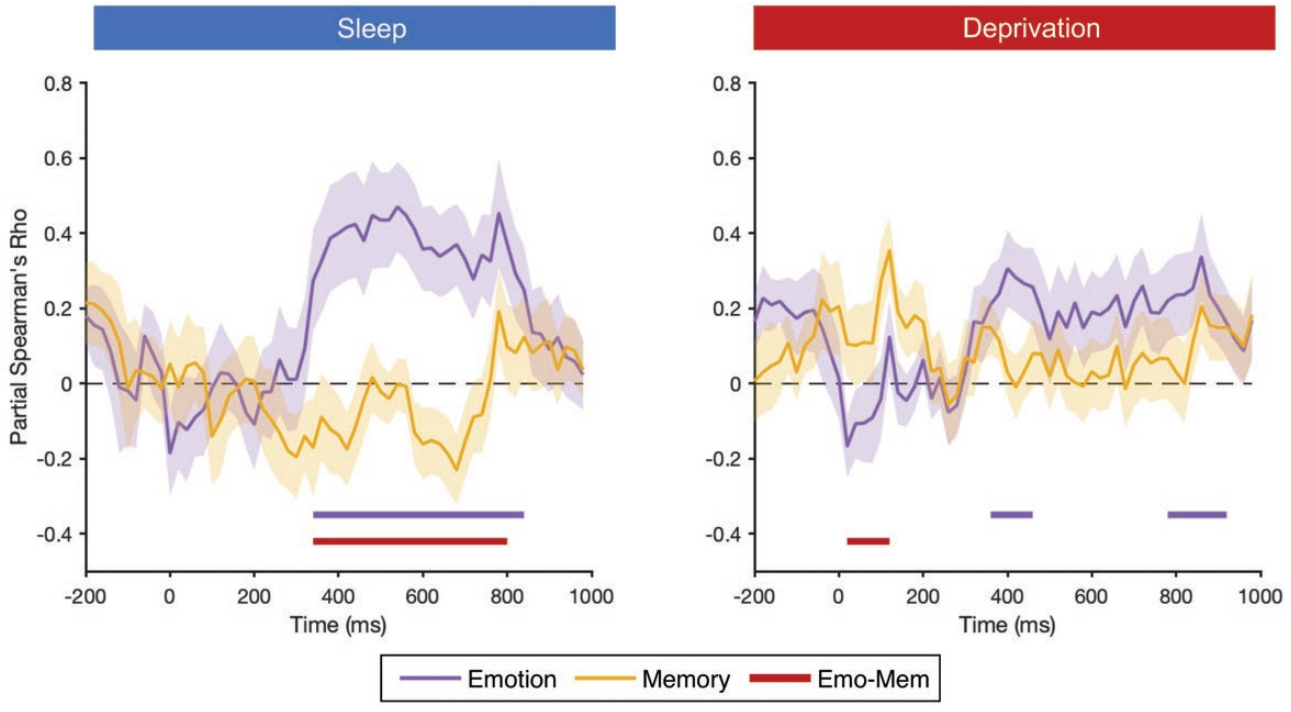


**Figure 5.** Time course of partial Spearman correlations (Fisher Z-transformed) between ERP decoding RDMs and model RDMs for sleep group (left) and sleep deprivation group (right). Horizontal lines below the plots indicate significant times: colored lines represent time points in which the partial spearman's rho significantly greater than 0 and red lines represent significant difference between conditions. Both controlled for multiple comparisons ($p < 0.05$). Shading indicates ±1 SEM.

sleep deprivation group recruited additional parietal LPC old-new effect. Multivariate whole-brain analyses further indicated that sleep led to a more stable representation of emotion than memory at delayed test, suggesting affect-focused processing in the long term. In contrast, the sleep deprivation group showed a largely indistinguishable representation between emotion and memory. Given comparable recognition performance between these two groups in the delayed test, univariate and multivariate ERPs analyses collectively suggested that sleep vs. sleep deprivation engaged different neurocognitive processes when re-exposed to emotional stimuli.

Sleep (vs. sleep deprivation) preserved memories independent of their emotion, as indicated by a presence of Group main effect and an absence of Group × Emotion effect in memory sensitivity ($d'$) and information accumulation speed ($v$) in the 12-h post-encoding test (note that the Group main effect of $v$ did not reach statistical significance). Although these findings stand in contrast to some previous studies using different experimental paradigms (e.g. a wakeful control group instead of a total sleep deprivation group) [3, 40–42], our results are largely consonant with studies employing sleep deprivation paradigms [11, 43–46]. Critically, our results are consistent with recent meta-analyses that synthesized comprehensive literature examining sleep's impact on emotional memories [9, 10]. Collectively, these pieces of evidence suggested that when compared to a total night of sleep deprivation that disrupts consolidation, sleep preserves both negative and neutral declarative memories. These results could be explained by the theoretical framework suggesting a differential role of non-rapid eye movement (NREM) and REM sleep in processing non-emotional and emotional memories. Notably, while NREM sleep may benefit the consolidation of non-emotional declarative memories via reactivation [47, 48]; REM sleep may specifically strengthen and modulate emotional memory through theta oscillations that originate from the amygdala, hippocampal, and neocortex that are involved in emotional memory processing [41, 46, 49–51]. Thus, overnight sleep involving both NREM and REM sleep cycles could result in a comparable consolidation of both negative and neutral memory observed in our study and the meta-analyses. A better understanding of the specific role of sleep stages on consolidation of emotional memories could be gained via direct manipulation of memories during specific sleep stages, as in the research using targeted memory reactivation [52, 53].

In terms of response biases, we found that slept participants were more liberal in responding to negative but not to neutral stimuli, while sleep-deprived participants did not show significant differences. Results from the sleep group aligned with previous research: in general, people are more likely to respond "old" to negative than to neutral stimuli, that is, a more liberal response bias, given the high survival value of negative stimuli [54]. Interestingly, sleep-deprived participants did not show this emotion-dependent response bias, possibly because sleep deprivation led to compromised discriminations between negative and neutral memories. Supporting this possibility, our exploratory analyses found that sleep-deprived participants rated negative pictures as less negative (i.e. toward neutrality) and less arousing, while neutral pictures as more negative and arousing relative to baseline ratings (see [11, 55] for similar results). Together, these findings suggest that a night of sleep deprivation impaired people's accuracy in affect judgments.

Focusing on memory changes, we found that sleep vs. sleep deprivation differentially influenced memory change as evidenced by the significant three-way interaction. Specifically, both negative and neutral memories declined in the sleep group, while only neutral memories declined but negative memories were preserved in the sleep deprivation group. Memory decline in the sleep group echoed previous studies that suggested a time-limited role of sleep in protecting declarative memories from decaying [56, 57]. Schönauer and colleagues reported that sleep-dependent benefits on declarative memories were only evident in the 12-h delay tests, but not in the 72- and 144-h tests [56]. Our study extends this finding by demonstrating sleep's short-term benefits on negative and neutral memories, followed by their decay. However, since we only had a 60-h post-encoding test, it remains unclear whether negative and neutral memories may have different forgetting curves following longer retention intervals, that is, 1 week or even years after encoding [2, 58]. Future studies could employ longer delays to gain a more comprehensive understanding of sleep's time-dependent retention of negative memories.

In the sleep deprivation group, negative memory remained unchanged (88% to 80% hit rates) while neutral memories significantly declined (89% to 76% hit rates) from 12- to 60-h post-encoding tests (see Table 6). Complementing memory performance, whole-brain decoding analyses also revealed stronger old/new classifications for negative than for neutral stimuli in the 3-day delayed test (see Supplement Figure S2, B). This finding is consistent with prior evidence that in the long term, sleep disruptions have smaller impacts on emotional than neutral memories [44, 58, 59]. Specifically, one study suggested that while sleep deprivation (vs. sleep) significantly impaired neutral memory 72-h post-encoding, participants from sleep deprivation and sleep groups performed equally well in recognizing negative memories [44]. Furthermore, Cellini et al. reported that poor sleep quality over a 1-week retention interval was correlated with better retention of negative memories [58]. Collectively, these results suggested that negative memories tend to be preserved in longer terms given disrupted sleep-based consolidation processes due to either poor sleep qualities or abrupt sleep deprivation. This may contribute to negative thinking/attribution styles observed among affective disorders that often co-occur with sleep disruption, for example, depression and anxiety [60–62].

ERPs further suggested that slept and sleep-deprived participants showed different neurocognitive processes underlying recognition of remote memories, as indicated by recollection-related LPC. While both sleep and sleep deprivation groups showed an early, frontal old-new FN400 effect (300–500 ms), only the sleep deprivation group showed the late parietal old-new LPC effect (600–1000 ms). These ERPs results fit the dual-process theory of memory recognition [63]: familiarity- and recollection-based retrieval processes contribute to memory recognition, with the early frontal FN400 indicating familiarity and the later parietal LPC indicating recollection [21, 22, 64–67]. Specifically, while familiarity leads to more automatic "know" judgments without retrieving episodic details, recollection involves more controlled retrieval of contextual information and resulted in "remember" judgments. Based on this evidence and the result that both groups achieved similar recognition performance, it is possible that for slept participants, memories were consolidated and well-integrated with the existing memory schema in the neocortex, which resulted in a familiarity-based FN400 effect

during recognition. However, in the sleep deprivation group wherein memory consolidation was disrupted, making an "old/new" judgment would require not only a sense of familiarity but also effortful retrieval of contextual details from learning episodes, as evidenced by both frontal FN400s and parietal LPCs.

It is worth mentioning that instead of indicating familiarity, FN400 may track implicit memory processes such as conceptual fluency/priming entailed in recognition judgments. Furthermore, LPC could also reflect familiarity-based memory judgments [68, 69]. Although our study was not designed to disentangle implicit vs. explicit memory processes, our findings clearly showed that sleep and sleep deprivation led to spatial-temporally distinguishable ERPs, and thus possibly different retrieval processes [22, 66].

Regarding memories' affective tones, we found that sleep (vs. sleep deprivation) preferentially preserved negative valence ratings in the short-term (see also [4, 5, 18, 51]); but led to more positive ratings in the longer term, that is, the "sleep to forget" affect depotentiation effect [19, 20]. These results aligned well with recent findings that sleep (vs. wake) led to attenuated affective responses to negative stimuli at one-week retests, [6] and with our recent study which found that sleep (vs. sleep deprivation) significantly reduced self-reported hyperarousal to highly aversive film scenes [70]. Together, these results suggested that multiple nights of sleep are important for affective charges to gradually dissipate. Note that the affect depotentiation effect documented here should be interpreted within the sleep group, as there were no significant between-group differences in the 60-h delayed tests. Future studies are warranted to examine more detailed temporal dynamics, for example, the time-dependent trajectory of affect change, how many nights of sleep are needed for the effect to emerge, etc.

While univariate analysis focuses on pre-defined ERPs, multivariate whole-brain analyses (e.g. decoding and RSA) can be more statistically powerful in parsing neural representations of emotion and memory in sleep and sleep deprivation groups. Our results revealed that whole-brain neural representations in both groups successfully distinguished emotion but not memory information, with the sleep group showing a numerically more pronounced and sustained emotion representation than the sleep deprivation group, though between-group differences were not significant. These results suggested that participants in the sleep group may prioritize the processing of affective tones of emotional memories, which may explain the ameliorated affective tones in the sleep group.

A few possible limitations warrant discussions. First, recognition accuracies were high in both groups (see Table 6). Strong memories in our recognition task may be the reason why we did not find sleep-based, preferential consolidation of emotional over neutral memories. Future studies should take into consideration of potential moderating factors such as memory strength (strong vs. weak) and tasks (recognition, recall). However, it should be noted that our findings were consistent with recent meta-analyses, which either aggregated studies using recall and recognition tasks [10] or solely analyzed recognition measures [9]. Second, participants were not constrained from taking naps after sleep deprivation manipulation. Given that daytime naps following deprivation may influence delayed behavioral performance, we included participants' self-reported nap durations from their sleep diaries in the analyses, with results suggesting that the recovery sleep did not influence our main findings (see details in Supplement). Consistently, a recent study suggested that even two nights of recovery sleep after one-night sleep deprivation cannot restore the episodic memory performance to the baseline level [71]. Nevertheless, future studies could control, preferably by monitoring recovery sleep following deprivation to fully understand its impact on affective/cognitive functions.

In sum, combining behavioral measures and uni-/multivariate EEG analyses, we provided novel insights on sleep and sleep deprivation's time-dependent impact on emotional memories and their affective tones. Even with comparable recognition performances at delayed tests, sleep and sleep deprivation engaged different retrieval processes and neural representations for emotion vs. memory processing. These results underscored the dynamic nature of sleep-dependent memory/affect changes and enriched our understanding of how sleep vs. sleep deprivation impacts the recognition of remote memories and the underlying neurocognitive mechanisms.

## Supplementary material

Supplementary results to this article can be found in the file "Supplementary Materials".

## Data Availability

Data and analysis scripts are available at https://osf.io/7m6fu/?view_only=95b6329543684c7f80379d98ec64e2be.

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