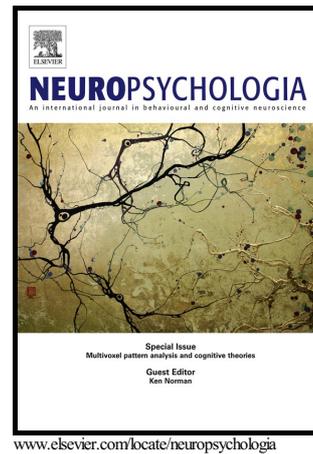


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Sleep divergently affects cognitive and automatic emotional response in children

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Abstract

Sleep enhances memory for emotional experiences, but its influence on the emotional response associated with memories is elusive. Here, we compared the influence of nocturnal sleep on memory for negative and neutral pictures and the associated emotional response in 8-11-year-old children, i.e., an age group with heightened levels of emotional memory-related sleep

features. During all sessions, emotional responses as measured by subjective ratings, the late positive potential of the EEG (LPP) and heart rate deceleration (HRD) were recorded. Sleep enhanced picture memory. Compared to dynamics across wakefulness, sleep decreased the emotional response in ratings and the LPP, while increasing the emotional response in HRD. We conclude that sleep consolidates immediate emotional meaning by enhancing more automatic emotional responses while concurrently promoting top-down control of emotional responses, perhaps through strengthening respective neocortical representations.

Keywords: sleep, emotion, EEG, memory

1. Introduction

Whereas research has revealed a benefit of sleep on emotional memory (e.g. Hu, Stylos-Allan, & Walker, 2006; Nishida, Pearsall, Buckner, & Walker, 2009; Wagner, Gais, & Born, 2001), sleep's influence on the emotional reactivity associated with a memory has produced complex and seemingly disparate results. Sleep has been shown to increase (Wagner, Fischer, & Born, 2002), decrease (Pace-Schott, et al., 2011; van der Helm, et al., 2011), and preserve (Baran, Pace-Schott, Ericson, & Spencer, 2012; Pace-Schott, et al., 2011; Werner, Schabus, Blechert, Kolodyazhniy, & Wilhelm, 2015) the emotional tone associated with memories. Interestingly, a central role of rapid eye movement (REM) sleep has consistently emerged, leading to two conflicting theories on its role in emotional processing. The Sleep to Forget, Sleep to Remember (SFSR) theory proposes that REM sleep specifically decreases emotional tone by providing an opportunity to process emotional memories within a neurochemical environment that supports memory consolidation in an emotionally neutral setting (Walker, 2009). The SFSR theory has received some support, with work suggesting REM physiology is linked to decreases in emotional tone (van der Helm, et al., 2011). The second theory proposes that REM sleep preserves emotional tone through consolidation of emotional salience (Baran, et al., 2012; Pace-Schott, et al., 2011; Werner, et al., 2015). In this framework, REM sleep is assumed to strengthen the link between a stimulus and its associated immediate emotional meaning (i.e., aversive or safe), thereby leading to more robust emotional responses to the stimulus. Emotional salience consolidation (ESC) might be associated with the enhanced consolidation of emotional memory seen across sleep.

Emotional scenarios elicit both physiological and behavioral responses. A prominent physiological response is the tendency of heart rate to decrease during confrontation with an

emotionally relevant stimulus (Margaret M Bradley, Codispoti, Cuthbert, & Lang, 2001). Encountering emotional stimuli also elicits an enhanced central nervous response, which can be measured as an increase in event-related response amplitude in the EEG (i.e. the late positive potential at Pz, see Cuthbert, Schupp, Bradley, Birbaumer, & Lang, 2000). While heart rate deceleration is more automatic in its features, in that it is preattentively triggered and directly controlled by subcortical structures like the amygdala and brainstem (Öhman, Hamm, & Hugdahl, 2000), the late positive potential (LPP) as well as the subjective emotional response (as assessed by ratings) are modulated by an interplay between the amygdala and prefrontal cortex (PFC, Hajcak, MacNamara, & Olvet, 2010; Ochsner, Silvers, & Buhle, 2012). Importantly, top-down cognitive processes readily influence both subjective ratings and the LPP (Dennis & Hajcak, 2009; Hajcak, et al., 2010).

Sleep's influence on emotional tone might depend on the nature of the emotional response considered, and more specifically, on the degree to which it is influenced by cognitive processes. The level to which the HRD differentially responds to emotional compared to neutral stimuli is preserved over a nap (Pace-Schott, et al., 2011) and HRD responses decrease after a night of sleep in an emotionally-independent manner (Cunningham, et al., 2014). Thus, more automatically triggered emotional responses might be preserved by sleep. However, more complex emotional response measures, which recruit cognitive processes to a greater extent, might become more accessible to top-down control and thereby decrease over sleep. While some evidence from emotional ratings supports this notion (van der Helm, et al., 2011), other studies examining sleep on subjective ratings measures have been contradictory (Baran, et al., 2012; van der Helm, et al., 2011; Wagner, et al., 2001). The LPP, as another measure integrating emotional top-down control, has thus far only been investigated in one sleep study where it was related to

the emotional enhancement in memory after REM-rich sleep (Groch, Wilhelm, Diekelmann, & Born, 2013).

Children are an excellent model of enhanced emotional processing during sleep as they exhibit heightened levels of a number of sleep features which have been associated with emotional memory processing in adults (i.e. REM & NonREM theta and delta power: Kurth, et al., 2010; Nishida, et al., 2009, and NonREM spindle density: Clawson, Durkin, & Aton, 2016; Kaestner, Wixted, & Mednick, 2013) and likewise a greater benefit of sleep on emotional memory consolidation than adults (Prehn-Kristensen, et al., 2013). What is more, they tend to have more emotional sleep experiences as evidenced by increased nightmare and night terror frequency (Simonds & Parraga, 1982). Though emotion robustly influences subjective ratings, LPP, HRD, and memory in children (Leventon, Stevens, & Bauer, 2014), the influence of sleep on the emotional tone associated with memories has not yet been reported in this age group.

We investigated how sleep influences emotional reactivity in 8-11 year olds. Children encoded negative and neutral pictures and then either stayed awake or slept in the laboratory during a 10-hour retention period. They then saw the original along with new pictures and were asked to report if they recognized each picture. During encoding and recognition testing, subjective (ratings of valence and arousal), central nervous (LPP of the brain evoked response) and autonomic nervous (HRD) system measures of the emotional response were assessed, whereby the emotional response was defined as the response difference between negative and neutral pictures. This metric provides a measure of emotional reaction strength that is corrected for possible differences in baseline reactivity (e.g. Coan & Allen, 2007; Phelps, et al., 2001). We expected that, compared to wake, measures of emotion that are subject to greater cognitive control would decrease after sleep, while measures of emotion that are less influenced by

cognitive control would be preserved. In addition, we hypothesized that consolidative influences of sleep (as measured by emotional response) would be specifically linked to REM sleep.

2. Methods

2.1 Participants

Sixteen healthy children without sleep disturbances between the ages of 8 and 11 years (mean \pm SD: 9.25 ± 1.06 years, 8 females) participated in the experiment. Sample size was based on a previous within-subjects study addressing the influence of sleep on emotional response in adults (Groch, et al., 2013). All participants were physically and mentally healthy according to parental report and the Child Behavior Checklist (Achenbach, 1991; Arbeitsgruppe Deutsche Child Behavior Checklist, 1998), and had normal or corrected-to-normal vision. Participants had an average digit span forward of 5.57 ± 1.26 and backward of 3.94 ± 1.18 according to the digit span subscale of the Wechsler Intelligence Scale (Petermann & Petermann, 2011). Participants did not exhibit sleep disturbances according to parent and child reports. The study was approved by the University of Tübingen medical faculty ethics committee and both parents and children gave informed verbal and written consent.

2.2 Experimental Design and Procedures

Recognition memory and emotional responses to pictures were compared between a Sleep and a Wake condition, following a within-subjects crossover design where each child was tested on both conditions with an interval of at least 12 days between the participant's conditions. The

order of conditions was randomly assigned to the children, with 9 children of the final sample of 16 children starting with Sleep condition. Each condition started with an Encoding session, where the task pictures were presented the first time, followed by a 10-hour retention period in which the child either slept or was awake, and then a Recognition session in which the original pictures were presented along with distractor pictures which had not been presented in the Encoding session (Figure 1C and D). In both sessions, valence and arousal ratings (collected with the self-assessment manikin, SAM; M. M. Bradley & Lang, 1994), the LPP, and HRD responses to the pictures were measured.

Each child participated in an adaptation session before the experiment proper. For this session, children and parents arrived at the lab at 18:00 h. Children filled out a questionnaire about their sleeping habits and completed the digit span task. They also practiced the control tasks, which were measured before each experimental condition, including a 5-minute version of the Psychomotor Vigilance Test (PVT, Roach, Dawson, & Lamond, 2006) to assess vigilance, the Stanford Sleepiness Scale (SSS, Hoddes, Zarcone, Smythe, Phillips, & Dement, 1973) to assess sleepiness, the Positive and Negative Affect Schedule (PANAS; Watson, Clark, & Tellegen, 1988) to assess mood, and a five-point Likert-scale assessing motivation (1 = absolutely not motivated, 5 = extremely motivated). During this time, parents were asked to fill out the questionnaires about the child's health and sleep behavior. Children were then prepared for bed and electroencephalographic (EEG), electrocardiographic (ECG), electromyographic (EMG), and electrooculographic (EOG) recordings. They then slept for ~9 hours to ensure acclimation to the conditions of the sleep laboratory.

For the Sleep condition, children and parents arrived ~3 hours before the child's habitual bedtime. Children prepared for bed and recording electrodes were applied (EEG, ECG, EMG and

EOG). Children performed the control and main tasks of the Encoding session and then went to sleep for ~9 hours. Upon waking, the children ate a light breakfast while electrode impedances were checked. It was ensured that the children were awake at least 30 minutes before beginning the Recognition session, in order to avoid any influences of sleep inertia on task performance.

For the Wake condition, children and parents arrived at the lab at ~7:30 h. The procedure was then identical to the Sleep condition with the exception of a day of wake during the retention period. Children wore an activity-tracking device (Actiwatch 2, Philips Respironics) to ensure that they did not sleep during the wake period and families were asked to abstain from strenuous activities over the course of the day. Participants ate a light meal before starting the Recognition session.

2.3 Materials and Task

A set of 444 pictures (taken from the International Affective Picture System, IAPS; Lang, Bradley, & Cuthbert, 2008, and other studies; Jackson, Meltzoff, & Decety, 2005; Prehn-Kristensen, et al., 2009) was used in this study to create two unique versions of the task (List A and B, order balanced) for the participant's two conditions. Each task version consisted of 72 negative targets and 72 neutral targets, in addition to 36 negative foils and 36 neutral foils which were used as distractor pictures during recognition (Figure 1D). An additional six positive pictures were included in each list with the sole purpose of maintaining motivation and were not included in the analyses. A pilot study, wherein a larger cohort of children ($n = 41$) used the Self-Assessment Manikin (SAM, M. M. Bradley & Lang, 1994) to rate the pictures, confirmed that children generally rated the negative pictures as more negative and more arousing (mean \pm sem

valence ratings: negative = $-1.68 \pm .75$, neutral = $.78 \pm .82$, $t(40) = -16.48$, $p < .001$; arousal ratings: negative = 4.58 ± 1.47 , neutral = 1.77 ± 1.18 , $t(40) = 12.32$, $p < .001$).

During the Encoding session, target pictures were presented in a pseudo-random order wherein consecutive iterations of picture category (i.e. negative and neutral) were limited to three. A single trial consisted of the following procession: a fixation circle (displayed for a randomized period between 1 and 2 seconds), the picture (displayed for 1.5 seconds), a blank screen (displayed for 6 seconds), valence rating (i.e. valence SAM with the question: “How unpleasant or pleasant did you feel while looking at the picture?”, coded from -5 to 5), arousal rating (i.e. arousal SAM with the question: “How calm or nervous did you feel while looking at the picture?”, coded from 1 to 9), and finally an inter-trial interval of 2 seconds (Figure 1D). At the Recognition session, target and distractor pictures were intermixed. The trial procession was identical except for the additional question (following the ratings): “Is this picture old or new?” to which children responded with either “Old” or “New.” Participants were instructed to rate all pictures based on their momentary feelings using a computer mouse and to not try to remember how they had rated a picture if they had seen it before. The task was presented using E-Prime® 3.0 (Psychology Software Tools, Inc., Sharpsburg, Pennsylvania, USA).

2.4 Behavioral Analysis

Recognition memory scores were calculated as recognition accuracy, i.e. hit rate minus false alarm rate, for negative and neutral pictures, separately. Average ratings for valence and arousal were calculated according to trial type, i.e. negative target at encoding, neutral target at encoding, successfully remembered negative target at recognition (negative hits), and successfully

remembered neutral target at recognition (neutral hits). Emotional response for all measures was calculated as the difference between the response to negative images and the response to neutral images at each session. This measure reflects the strength of an emotional response while correcting for possible differences in baseline reactivity. The analysis was limited to trials where the picture was correctly remembered (hits) in recognition sessions.

2.5 Electrophysiological Recordings and Analysis

Electrophysiological data was collected using Brain Vision hardware and software (Brain Products GmbH, Gilching, Germany). During all sessions, EEG was recorded at F3, Fz, F4, C3, Cz, C4, P3, Pz, and P4 (referenced to linked mastoids with FC1 and FC2 as grounds) according to the 10-20 system using Ag/Cl electrodes. Two diagonally placed EOG electrodes were used to measure eye movements. ECG bipolar electrodes were placed on the lower left and upper right chest. Signals were sampled at 500 Hz, and EEG electrode impedance was kept below 5 k Ω .

Event-related potential (ERP) processing was performed with the Brain Vision Analyzer 2.0 Software (Brain Products GmbH, Gilching, Germany). EEG and EOG were first filtered between 0.3 and 35 Hz using a zero-phase Butterworth filter (24 dB/oct) with a 50 Hz notch. Trials were segmented from -200 ms before picture onset to 1500 ms after picture onset and then subjected to linear detrending according to Hennighausen et al. (Hennighausen, Heil, & Rösler, 1993). Baseline correction of the ERP segments was performed using the 200 ms before picture onset. ERP segments were rejected as artifactual when 1) a gradient $> 40 \mu\text{V}/\text{ms}$ was detected, 2) a voltage difference $> 150 \mu\text{V}$ occurred within the 1700-ms segment, 3) a period of low activity ($< 0.5 \mu\text{V}$) was detected for a period > 100 ms, or 4) an ocular artifact was apparent by visual

inspection. ERP analyses concentrated on the LPP whose amplitude was taken as the peak voltage at Pz between 600 ms and 1000 ms after the picture onset (using the average voltage in this latency bin yielded essentially the same results and are not reported here).

To determine heart rate deceleration (HRD), R waves of the QRS complexes were first marked using a slope-based detection algorithm in the Brain Vision Analyzer 2.0 Software. Trials were extracted according to type and then visually inspected to exclude artifacted data. The maximum R-R interval in the 5-s interval following picture onset was subtracted from the mean R-R interval during the 1.5-s baseline period before picture onset. LPP and HRD responses were averaged according to trial type (negative and neutral targets at encoding, negative and neutral hits at recognition, see Figure 2 for traces of the original LPP and HRD signals).

Sleep EEG and EOG were filtered in the same manner as the ERP data. EMG was filtered with the same parameters but with a higher bandpass frequency range (5-100 Hz). Sleep recordings were scored according to standard criteria (Rechtschaffen, 1968) to obtain the time spent in different sleep stages (wake, stages 1, 2, slow wave sleep [SWS], and REM sleep in minutes and percentage of total sleep time [TST]). The Brain Vision Analyzer 2.0 Software was used to process and calculate power in the delta and theta bands during NonREM (S2 and SWS) and REM, respectively. Artifact-free sleep epochs were cut into 6-second segments with 2 seconds of overlap. A fast fourier transform using a symmetric Hanning window was used to calculate power with a 0.2 Hz resolution. Relative EEG power (%) at Fz (as done in previous work: Prehn-Kristensen, et al., 2013) was then calculated for each subject by dividing the power in each frequency bin by the total power in the spectrum for a specific sleep stage and multiplying by 100. Because frequency band ranges can vary widely from person to person (e.g. Klimesch, Russeger, Doppelmayr, & Pachinger, 1998; Pfurtscheller & Lopes da Silva, 1999),

we fine-tuned the determination of frequency ranges for the bands of interest by visually determining for each participant the peak frequency for the delta and spindle bands for NonREM sleep as well as theta during REM sleep, and centering the band limits around this peak (Supplementary Figure S2). This procedure resulted in the following average bands: 0.4-2 Hz for the NonREM sleep delta band, 10.5-13.2 Hz for the NonREM sleep spindle band, and 4.6-6 Hz for the REM sleep theta band.

To detect discrete spindles, EEG was bandpass filtered within a subject-specific spindle frequency range and spindle events were detected according to an established thresholding algorithm (see Gais, Mölle, Helms, & Born, 2002 for details). Subject-specific spindle bands were visually identified as the peak within the 9 to 15 Hz range (see Kurdziel, Duclos, & Spencer, 2013). Spindle counts were averaged over C3, Cz, and C4, similar to Kaestner et al. (2013). Spindle density was calculated as the average number of spindles per 30-second epoch for S2 sleep and SWS.

2.6 Statistical analyses

Physiological emotional response data from one participant had to be excluded due to a technical failure. Ratings from two participants were excluded from analyses because of performance values exceeding ± 2 standard deviations from the sample mean, suggesting that they may have responded randomly to the subjective rating portion of the task. It was nevertheless confirmed that they adequately performed the memory task (i.e. recognition accuracies $>65\%$). The sleep electrophysiology from frontal electrodes in one participant had to be excluded due to

technical problems with the recordings. Data of 3 participants were excluded from LPP analyses due to values that exceeded ± 2 standard deviations from the mean.

Following the experimental within-subject cross-over design of the study, changes in memory and emotional response were analyzed using repeated measures analysis of variance (ANOVA) with the within-subjects factor Sleep (Wake vs. Sleep). The influence of sleep on recognition accuracy was addressed using an additional Emotion category (negative vs. neutral) within-subjects factor. For the analysis of emotional response, additionally, a within-subjects Session factor (Encoding vs. Recognition) was introduced. Bonferroni-corrected paired *t*-tests were used to follow up significant ANOVA effects (new α -level for comparison: $.05/2$ tests = $.025$). To determine the specific nature of the influence of sleep, change scores in response over the retention interval (defined by the difference between the respective response at recognition minus the response at encoding) were calculated separately according to picture class (negative and neutral) whenever a significant interaction between Sleep and Session was found (Bonferroni-corrected paired *t*-tests as described above).

Pearson's correlations were used to test for relationships between sleep features that have been associated with emotional preservation (REM% [Wagner, et al., 2001], REM theta power [Prehn-Kristensen, et al., 2013], S2 and SWS spindle density [Kaestner, et al., 2013]) and measures which did not exhibit a change in emotional response over sleep (LPP and HRD, calculated as emotional response at recognition minus emotional response at encoding) as well as emotional differentiation in memory (i.e. the difference between negative recognition accuracy and neutral recognition accuracy). We also tested for whether emotional response measures which were preserved over sleep correlated with emotional differentiation following sleep or wake.

Bonferroni correction was applied such that the required α -level for significance was $.05/16$ tests = $.003$.

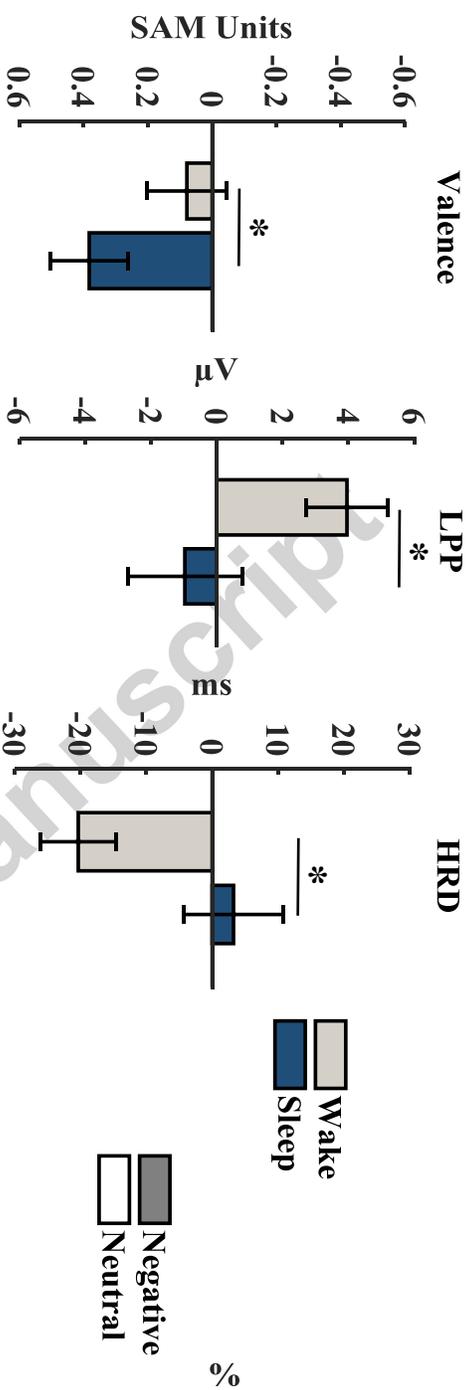
Influences of sleep on control variables were addressed using a Sleep x Session ANOVA. Because this study was focused on possible influences of sleep on emotion and memory, follow up correlations were calculated between control variables exhibiting Sleep effects (main effects or interactions) and the independent variables of interest (emotional memory and emotional response for each measure).

3. Results

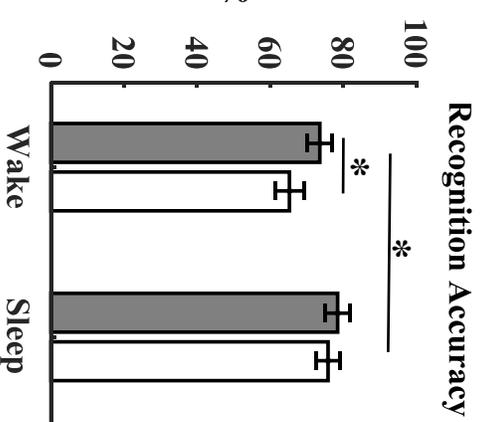
3.1 Recognition Memory

In general, participants correctly recognized more target pictures when they had slept after the encoding session than when they had stayed awake (Sleep main effect for recognition accuracy: $F(1,14) = 8.52$ $p = .01$, $\eta_p^2 = .38$, Figure 1B). Also, negative images were generally better recognized than neutral ones (Emotion main effect: $F(1,14) = 17.51$ $p = .001$, $\eta_p^2 = .56$). However, whereas better recognition accuracy for negative compared to neutral pictures was found after staying awake ($p = .001$), this was not the case for the Sleep condition ($p = .14$, Sleep x Emotion interaction: $F(1,14) = 6.17$, $p = .026$, $\eta_p^2 = .31$), possibly reflecting a ceiling effect of the generally enhanced recognition performance in the Sleep condition.

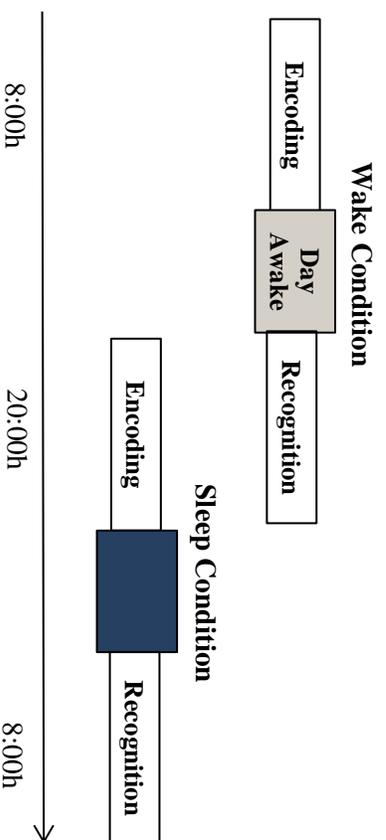
A) Change in Emotional Response



B) Recognition Accuracy



C) Experimental Design



D) Emotional Picture Task

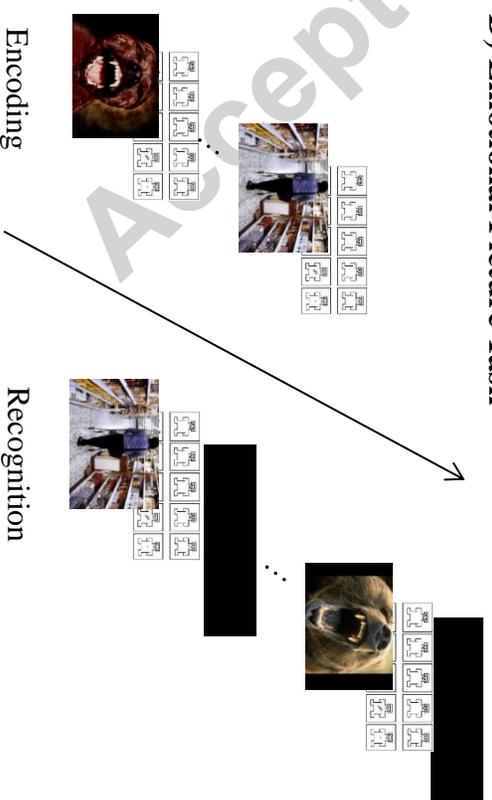


Figure 1. A) Sleep and wake intervals differentially affected the change in emotional response from encoding to recognition. Whereas sleep decreased emotional response in valence ratings, the ratings did not change across the wake interval. (Note that the y-axis has been inverted to facilitate interpretation of the valence response: a positive change is a decrease in emotional response, $n = 14$). The emotional response of the late positive potential (LPP) of the event-related EEG at Pz increased over a day of wake but was preserved over a night of sleep. Therefore, relative to wake, sleep decreased the emotional response in LPP ($n = 12$). The emotional response in heart rate deceleration (HRD) decreased over the wake interval but was stable after a night of sleep. Thus, relative to wake, sleep increased the emotional response in HRD ($n = 15$). B) Sleep enhanced recognition accuracy in general, while wake led to better memory for negative compared to neutral pictures ($n = 16$). C) A recognition task was used in a within-subjects crossover design to examine the influence of post-encoding sleep vs wakefulness on memory and associated emotional responses in 8-11 year old children. During Encoding, children viewed emotional pictures in either the evening (Sleep condition) or the morning (Wake condition). After a 10-hour retention interval, children performed a memory task during the Recognition session. During both sessions, subjective ratings, the LPP of the EEG, and HRD were measured. D) During Encoding, children saw negative and neutral images that they rated with regard to subjective valence and arousal using the SAM. During Recognition, children saw the original images as well as negative and neutral distractors. Trials were identical to the Encoding session, with the exception of the additional question “Is this picture old or new?” which was asked after subjective ratings were performed. * represents $p < .05$.

3.2 Subjective Emotional Response

Children rated negative images as more negative and more arousing at both the Sleep (valence ratings: negative = $-1.88 \pm .78$, neutral = $.56 \pm .55$, arousal ratings: negative = 5.8 ± 1.36 , neutral = 2.44 ± 1.31) and Wake (valence ratings: negative = $-1.80 \pm .79$, neutral = $.47 \pm .40$, arousal ratings: negative = 5.43 ± 1.68 , neutral = 2.39 ± 1.02) encoding sessions (all p s < .001). Sleep decreased the emotional response (response to negative images minus response to neutral images) as measured by valence ratings of the successfully remembered pictures ($p = .007$). In contrast, valence ratings remained unchanged across a retention interval containing wake ($p = .53$, see Figure 1A for visualized Sleep x Session interaction: $F(1,13) = 4.78$, $p = .048$, $\eta_p^2 = .27$; Sleep main effect: ns; Session main effect: $F(1,13) = 5.32$, $p = .038$, $\eta_p^2 = .29$; see Figure S3 in the Supplementary Material for emotional response at encoding and recognition, separately). Calculating change scores (response at recognition minus response at encoding) separately for neutral and negative images revealed that this interaction was driven by the fact that sleep produced a less negative rating of negative images (mean difference \pm sem: $+0.19 \pm 0.13$, see Supplementary Figure S4) and, simultaneously, a more negative valence rating of neutral images (-0.18 ± 0.06 , $t(13) = 3.17$, $p = .007$) whereas no such changes were observed across the wake retention interval (negative: -0.02 ± 0.10 , neutral: -0.10 ± 0.08 , $p = .53$). Arousal ratings exhibited a similar pattern of decreased emotional response across Sleep compared with the Wake condition, albeit less robustly (Sleep x Session interaction: $F(1,13) = 4.30$, $p = .058$, $\eta_p^2 = .25$, Sleep & Session main effects: ns). The influence of sleep on rating behavior did not appear to be driven by circadian effects, as the subjective emotional response did not significantly differ between the wake encoding session, which took place in the morning, and sleep encoding session, which took place in the evening (valence: $p = .16$; arousal: $p = .11$).

3.3 LPP Emotional Response

The emotional response as measured by the LPP of the event related potential at Pz remained stable across sleep ($p = .59$) but increased over the course of the wake period ($p = .008$; Sleep x Session interaction: $F(1,11) = 5.34$, $p = .041$, $\eta_p^2 = .33$; Sleep and Session main effects: ns). Thus, compared with the dynamics across the wake period, sleep led to a relative decrease in the LPP emotional response (see Figure 1A for visualized Sleep x Session interaction). Correspondingly, separate change scores for negative and neutral pictures indicated that the LPP slightly increased across sleep regardless of emotional picture category (negative: $2.81 \pm 1.61 \mu\text{V}$, neutral: $3.78 \pm 1.10 \mu\text{V}$, $p = .60$), whereas the wake period produced a particularly strong increase in LPP to negative pictures ($6.9 \pm 0.85 \mu\text{V}$) as compared to neutral pictures ($2.95 \pm 1.00 \mu\text{V}$, $t(11) = 3.21$, $p = .008$). The emotional response tended to be smaller at encoding in the morning (Wake condition) than at encoding in the evening session (Sleep condition; $p = .063$) suggesting that the increase in emotional response in LPP across sessions in the Wake condition may partially reflect a circadian influence (see Figure S3 for an overview of the emotional responses of the LPP at encoding and recognition, as well as additional LPP analyses in the Supplementary Material). To explore this possibility, we removed the three participants with the lowest emotional response at the wake encoding session in order to match emotional response at encoding ($t(8) = -1.49$, $p = .175$). This analysis revealed essentially the same pattern with a statistical trend for the Sleep x Session interaction ($F(1,8) = 3.93$, $p = .083$, $\eta_p^2 = .33$), which suggests that time of day alone did not exclusively drive the resultant data patterns.

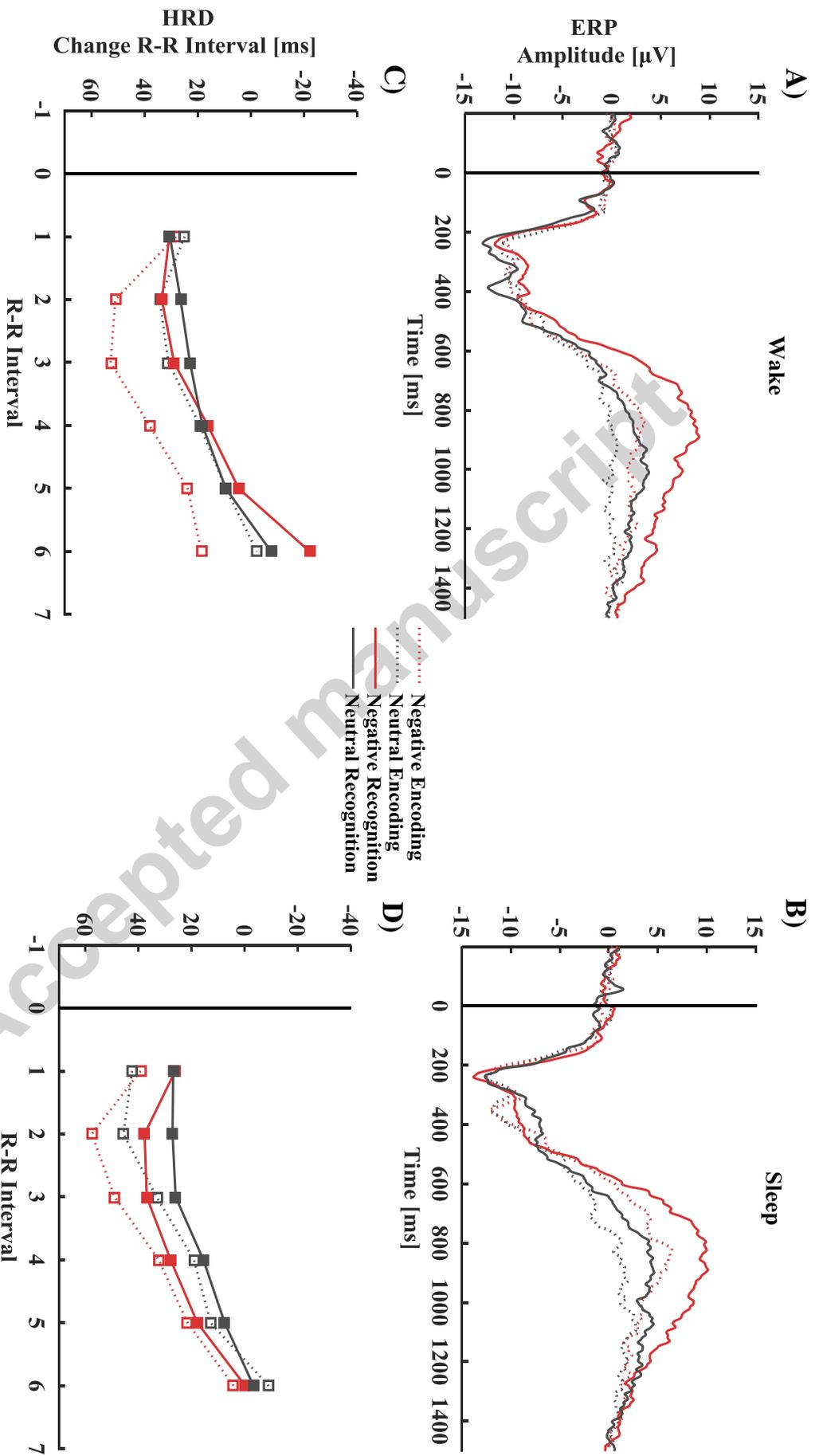


Figure 2. The influence of sleep on physiological measures of emotion. A) and B) show grand average LPP traces at Pz across wake and sleep, respectively. C) and D) show the change in R-R interval relative to the 1.5s baseline period before image onset (post onset minus pre onset). Note that a positive change R-R interval represents a deceleration in heart rate and that the y-axis has been inverted to facilitate interpretation of the heart response. Black vertical lines represent image onset.

3.4 HRD Emotional Response

In contrast to subjective ratings and LPP, the HRD emotional response decreased across wake ($p = .003$) but not across sleep ($p = .67$; Sleep x Session interaction: $F(1,14) = 5.20$ $p = .039$, $\eta_p^2 = .27$, Sleep and Session main effects: ns). Thus, compared with the dynamics across the wake period, sleep led to relative increase in HRD emotional response (see Figure 1A for visualized Sleep x Session interaction). Analysis of separate change scores for negative and neutral pictures revealed that this interaction was driven by a decrease in HRD response to the negative pictures (mean \pm sem: -14.09 ± 6.81 ms, $t(14) = -3.54$, $p = .003$, see Supplementary Figure S4) but not neutral pictures (6.24 ± 6.85 ms) across the wake retention interval, whereas across sleep HRD decreased regardless of emotional picture class (negative: -15.73 ± 10.72 ms, neutral: -18.97 ± 8.23 ms, $p = .91$). HRD responses were comparable for the Encoding sessions of the Sleep and Wake conditions ruling out substantial circadian effects ($p = .13$; see Figure S3 in the Supplementary Material).

3.5 Correlations Between Emotional Response, Sleep Parameters and Memory

The overnight change in the emotional HRD response (emotional response to hits at recognition minus emotional response at encoding) positively correlated with the degree of emotional memory differentiation after sleep ($r = .75, p = .001$): participants who showed a relative increase in HRD emotional response also showed a bigger difference between negative and neutral recognition accuracy. No other correlations survived multiple testing correction at $\alpha = .003$.

3.6 Sleep Parameters and Control Variables

Sleep scoring of the polysomnographic recordings from the experimental night indicated that the children slept normally (Supplementary Figure S1). In total, they slept around 8.58 hours. Participants spent approximately 19.9 minutes, 162.8 minutes, 225.1 minutes and 99.6 minutes in sleep stages 1, 2, SWS, and REM, respectively. They entered SWS after ~4.5 minutes and REM after ~95 minutes. Participants were awake for approximately 6.2 minutes after sleep onset.

Results from control tests are summarized in Supplementary Table 1. Motivation, vigilance, negative mood, and sleepiness in the Encoding and Recognition sessions were not differentially influenced by the Sleep and Wake conditions ($ps > .26$, for the respective main and interaction effects). Motivation was higher during the Encoding sessions than the Recognition sessions (Session main effect: $F(1,15) = 4.77, p = .045$). Positive mood (PANAS-Positive) exhibited a similar trend (Session main effect: $F(1,15) = 3.99, p = .064$), and was higher during the Sleep than Wake condition (Sleep main effect: $F(1,15) = 7.82, p = .014$). There were no consistent correlations between PANAS-Positive scores and any of the emotional response or memory

measures ($ps \geq .059$), excluding any substantial contributions of this factor to the effects of sleep on emotional responses or recognition performance.

4. Discussion

Beyond confirming that sleep enhances memory for pictures (e.g. Baran, et al., 2012), our study in ~10 year old children revealed a distinct pattern of sleep effects on the emotional response associated with these memories. Compared with a period of daytime wakefulness, nocturnal sleep decreased the emotional response as measured by behavioral ratings (valence) and the LPP (by preserving a response that would otherwise increase over wake) while increasing the emotional response as measured by HRD (by preserving a response that would otherwise decrease over wake). It therefore appears that sleep decreases responses that are more subject to cognitive control, while increasing responses that are generated more automatically (i.e. less sensitive to top-down influences).

This study provides support for the body of research showing that sleep enhances memory (Diekelmann & Born, 2010), though it should be considered that without an immediate recognition test after encoding it is impossible to tell whether encoding strength was influenced by time of day. It should be noted, however, that many studies which included immediate recognition sessions in order to control for circadian influences show a similar improvement in memory performance after sleep (e.g. Prehn-Kristensen, et al., 2013). Unlike previous studies (Hu, et al., 2006; Nishida, et al., 2009; Prehn-Kristensen, et al., 2009) we did not find a preferential enhancement of negative over neutral stimuli by sleep. This discrepancy likely

reflects a ceiling effect, as average hit rates for negative pictures in the Sleep condition reached a maximum of 91%.

Our finding that sleep decreased emotional response in valence ratings in children, together with previous findings in adults from van der Helm et al. (2011), suggests that sleep leads to a decrease in the explicit judgment of the aversiveness of a stimulus. Overall, however, studies of the effects of sleep on valence ratings to negative stimuli reveal a rather heterogeneous picture (Baran, et al., 2012; Wagner, et al., 2002), likely reflecting the complex integration of physiological signals and concurrent behavioral goals that are inherent to cognitive emotional appraisals (Schachter & Singer, 1962). Such aspects of cognitive control may be more sensitive to subtle changes in experimental context or the composition of sleep.

The effects of sleep on valence ratings were paralleled by a relative decrease in the emotional LPP response across sleep when compared to wakefulness. Specifically, the emotional LPP response remained at a rather constant level across sleep, while increasing across wake. Though it should be emphasized that circadian factors may have partially influenced this pattern, these results are in accordance with functional magnetic resonance imaging (fMRI) work reporting a decrease in emotional reactivity as measured by amygdala activity across sleep (van der Helm, et al., 2011). Importantly, both the LPP and amygdala activity have been linked to emotional reactivity and prefrontal cortex-driven emotion regulation in children and adults (Babkirk, Rios, & Dennis, 2015; Dennis & Hajcak, 2009; Hajcak, et al., 2010; Ochsner, et al., 2012). The relatively diminished LPP after sleep therefore likely reflects increased emotion regulation which itself might be a consequence of a sleep-induced enhancement of the cortical representation of the stimulus (Gais, et al., 2007; Liu, et al., 2016; Takashima, et al., 2006).

Opposing the down-regulating effects of sleep on the emotional response in subjective ratings and LPP, sleep produced a relative enhancement in the emotional heart rate deceleration (HRD) response compared to dynamics across wake. Specifically, sleep was associated with preservation of emotional HRD response, which otherwise decreased across wake. Our findings in children agree with previous findings in an adult study which likewise showed that HRD in response to emotional pictures decreases across wake but is preserved across a nap (Pace-Schott, et al., 2011). Change scores also confirmed that the preserving effect of sleep on HRD accompanied a stimulus category-independent decrease in HRD across sleep, as seen in adults (Cunningham, et al., 2014).

Interestingly, even though a ceiling effect was seen in our memory measure, the degree of emotional memory enhancement and the degree of emotional HRD response preservation across the retention period were positively correlated in the Sleep but not Wake condition. This suggests that a similar underlying mechanism is responsible for preserving the emotional HRD response and emotional memory, and in extension, that the immediate emotional meaning of an event is inherently intertwined in the memory representation. Previous work has shown that the enhanced consolidation of the entirety of an emotional memory is linked to REM sleep (Menz, Rihm, & Büchel, 2016), however, in our study respective correlations for REM% and REM sleep theta power with emotional preservation did not reach significance after correction for multiple tests.

Our study is unique in showing that rather than exerting a uniform influence, a night of sleep differentially affects automatic and cognitive aspects of the emotional response. In combination, the present findings suggest a scenario in which sleep affects memory and the associated emotional response via two different mechanisms: On the one hand, sleep preserves the immediate emotional meaning of events, leading to preservation of automatic emotional

responses like HRD. On the other hand, sleep generally acts to strengthen declarative components of a memory in a way that may also make them more accessible to retrieval and various other cognitive functions. This episodic memory consolidation process leads to the strengthening of the neocortical representation of the event and has been linked to NonREM sleep, as well as the associated slow wave and spindle activity (Diekelmann & Born, 2010). Indeed, recent work has shown that overnight consolidation of emotional memories is associated with preservation of autonomic emotional reactivity and reorganization of memory-associated activity from hippocampal to neocortical structures (Liu, et al., 2016). The strengthening of respective cortical representations might improve the top-down control of emotional responses, seen here as diminished ratings of negative valence and a relative decrease in the emotional LPP response after sleep.

Such a twofold influence of sleep - preserving automatic emotional response and enhancing top-down control of emotional response - might help to bridge the divergent predictions of the ESC and the SFSR theories that have been proposed to explain effects of sleep on emotional memory (Baran, et al., 2012; Pace-Schott, et al., 2011; Walker, 2010; Werner, et al., 2015). In support of the ESC theory we found that sleep increases (via preservation of a response that would otherwise decrease over wake) emotional responses that are more automatic in nature (HRD). In support of the SFSR theory, we found that sleep leads to a relative decrease in more cognitive emotional responses, i.e. those that may employ top-down regulation mechanisms like subjective ratings and the LPP (via an absolute decrease in valence ratings and preservation of the LPP response which otherwise increases over wake). Thus, our study shows that rather than acting as a uniform entity, emotional response emerges from the interaction between automatic emotional reaction systems and cognitive processes, each of which is divergently influenced by sleep.

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Conflict of Interest Statement:

The authors declare no competing financial interests.

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Highlights

- Sleep divergently influences different levels of emotional processing of memories
- Sleep consolidates emotional meaning of stimuli by enhancing automatic responses
- Sleep decreases emotional responses associated with top-down cognitive control

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