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Dissociating the contributions of slow-wave sleep and rapid eye movement sleep to emotional item and source memory

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ABSTRACT

Sleep benefits the consolidation of emotional memories, and this influence is commonly attributed to the rapid eye movement (REM) stage of sleep. However, the contributions of sleep stages to memory for an emotional episode may differ for the event per se (i.e., item memory), and the context in which it occurred (source memory). Here, we examined the effects of slow wave sleep (SWS) and REM sleep on the consolidation of emotionally negative and neutral item (picture recognition) and source memory (recall of picture-location and picture-frame color association) in humans. In Study 1, the participants ($n = 18$) learned 48 negative and 48 neutral pictures which were presented at specific locations and preceded by colored frames that had to be associated with the picture. In a within-subject design, learning was either followed by a 3-h early-night SWS-rich or by a late-night REM sleep-rich retention interval, then retrieval was tested. Only after REM-rich sleep, and not after SWS-rich sleep, was there a significant emotional enhancement, i.e., a significantly superior retention of emotional over neutral pictures. On the other hand, after SWS-rich sleep the retention of picture-frame color associations was better than after REM-rich sleep. However, this benefit was observed only for neutral pictures; and it was completely absent for the emotional pictures. To examine whether this absent benefit reflected a suppressive effect of emotionality on associations of minor task relevance, in Study 2 we manipulated the relevance of the picture-frame color association by combining it with information about monetary reward, following otherwise comparable procedures. Here, rewarded picture-frame color associations were equally well retained over SWS-rich early sleep no matter if the frames were associated with emotional or neutral pictures. Results are consistent with the view that REM sleep favors the emotional enhancement of item memory whereas SWS appears to contribute primarily to the consolidation of context-color information associated with the item.

1. Introduction

Emotional memories are remembered better than neutral memories (LaBar & Cabeza, 2006; McGaugh, 2000) and there is also a preferential consolidation of emotional over neutral memory during sleep (Payne & Kensinger, 2011; Van der Helm & Walker, 2009; Wagner, Hallschmid, Rasch, & Born, 2006). This memory benefit for emotional relative to neutral content has been termed "emotional enhancement" and is used here – as in previous studies – as a measure to specifically define emotional memory (LaBar & Cabeza, 2006; Payne & Kensinger, 2011; Wagner, Gais, & Born, 2001). The emotion-induced improvement of long-term memory has been linked to increased amygdala and parahippocampal activation present during encoding as well as during rapid eye movement (REM) sleep (Kensinger & Schacter, 2006; Maquet et al., 1996; Miyauchi, Misaki, Kan, Fukunaga, & Koike, 2009; Nofzinger, Mintun, Wiseman, Kupfer, & Moore, 1997), in addition to qualitative changes in the emotional memory retrieval network after sleep (Payne & Kensinger, 2011). Studies, which have mostly examined recognition-based item memory, revealed that EEG theta activity (4–8 Hz) during REM sleep correlates with emotional memory gains after sleep (Hu, Stylos-Allan, & Walker, 2006; Nishida, Pearsall, Buckner, & Walker, 2009; Popa, Duvarci, Popescu, Léna, & Paré, 2010). Studies using a split-night design demonstrated an emotional enhancement effect, i.e. a superior free recall of emotional compared to neutral text materials, specifically after a 3-h post-learning interval during the late night filled with

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REM-rich sleep, but not after an early-night period of sleep rich in slow wave-sleep (SWS) or after retention intervals of wakefulness (Groch, Wilhelm, Diekelmann, & Born, 2013; Wagner et al., 2001). Thus, REM sleep seems to play a role in emotional memory formation leading to better retention of emotional as compared to neutral content.

Emotional arousal can increase both memory of the object itself, i.e., familiarity-based item memory, as well as memory of the spatiotemporal context the object is presented in, i.e., source memory (Mather & Nesmith, 2008; McIntyre, Power, Roozendaal, & McGaugh, 2003). However, with regard to source memory, there is also notable evidence that an effect in the opposite direction can occur under specific conditions commonly known as weapon focus, i.e., for an arousal-induced inhibition of contextual memory formation (Loftus, Loftus, & Messo, 1987; Mather, 2007; Steblay, 1992). Here, a central emotional object in the foreground of a scene is preferentially remembered at the expense of peripheral background information, reflecting an emotion-induced impairment of contextual binding. The selective consolidation of emotional item over neutral associated source information is promoted by sleep (Payne, Chambers, & Kensinger, 2012; Payne, Stickgold, Swanberg, & Kensinger, 2008; see e.g., Lewis, Cairney, Manning, & Critchley, 2011, for findings that, the other way around, emotional context information does not seem to selectively influence sleep-related consolidation of associated neutral items). However, the specific contributions of sleep stages to this process remain enigmatic. Indeed, selectivity in sleep-dependent consolidation based on the criterion of future relevance of information (rather than emotionality) has been linked to SWS rather than REM sleep-related memory processing (Diekelmann & Born, 2010; Bendor & Wilson, 2012; Wilhelm et al., 2011). There are also hints that SWS is involved in the strengthening of contextual source information for both neutral materials (Drosopoulos, Wagner, & Born, 2005; Drosopoulos, Windau, Wagner, & Born, 2007; Wilhelm, Wagner, & Born, 2011) as well as for emotional materials (Groch et al., 2011).

Here, we aimed to dissect the roles of REM sleep and SWS in memory consolidation of emotional and neutral items, i.e., the pictures, and their associated context information, i.e., specifically the location of the picture on a computer screen and the color of a frame that preceded the presentation of the picture. We hypothesized that REM sleep supports emotional enhancement of item memory and SWS consolidates associated source information. Study 2 set out to further explore whether effects of sleep stages on the consolidation of context-color information depend on the relevance of the picture-context association. To this end, the presentation of the colored frame preceding the picture was combined with information about a monetary reward that would be received for later correct recall of the picture-frame-color associations, making the frame-color more salient and immediately task relevant.

2. Methods

2.1. Participants

Two studies were conducted, with 18 participants (mean age: 21.27 yrs, range 18–26 yrs; 12 women) taking part in the main experiment (Study 1) and 18 different participants (22.11 yrs, range 19–25 yrs, 10 women) taking part in an additional experiment (Study 2). Participants were native German speakers, non-smokers, free of medication, had no history of neurological, psychiatric or endocrine disorders, and followed a normal sleep-wake rhythm (i.e., no shift work, usual sleep time 2300–0700 h) for at least four weeks before the experiments. Prior to the experiments, subjects were accustomed to sleeping under laboratory conditions during an adaptation night, including attachment of electrodes for polysomnographic recordings. On experimental days they were required to get up at 0700 h and not to consume caffeine or alcohol. The study was approved by the ethics committee of the University of Luebeck and all participants gave written informed consent prior to participation.

2.2. Design and procedure

Fig. 1A illustrates the design of Study 1. The study was conducted according to a within-subject cross-over design with the order of conditions ("early sleep" vs. "late sleep") balanced across participants, and an interval of at least two weeks between the participant's two conditions. Participants reported to the lab at 2100 h for the early night condition and at 2200 h for the late night condition. Each condition started with the attachment of electrodes. For the early sleep condition, participants learned the task between 2200 and 2240 h (learning phase). This "learning phase" included an immediate (baseline) recall test 5 min after the learning proper. A 3-h retention period of sleep followed (lights off 2300 h), which was expected to be rich in SWS. Thereafter, in the retrieval phase (0300–0340 h), delayed task recall was tested. In the late sleep condition, participants first slept for about 3 h (starting 2300 h) before the learning phase (0300–0340 h) took place (with the learning phase again including an immediate recall test 5 min after learning). Then, a 3-h retention interval of REM sleep-dominated sleep followed (lights off 0400 h). The retrieval phase took place between 0800 and 0840 h.

Thus, the retention intervals in the two experimental conditions were characterized by either high amounts of SWS (early sleep) or high amounts of REM sleep (late sleep), with the start of the 3-h period being determined by sleep onset. After 3 h, participants were awakened as soon as they entered sleep stage 1 or 2 and subsequent testing was timed 45 min later to allow the participant to recover from sleep inertia. Awakenings from SWS and REM sleep were avoided to exclude confounding effects on memory performance by prolonged sleep inertia (e.g., Stones, 1977). Before each learning phase subjects indicated their level of sleepiness on a scale from 1 (active, alert) to 7 (very sleepy) (Stanford Sleepiness Scale, SSS; Hoddes, Dement, & Zarcone, 1972) and performed a 5-min version of the Psychomotor Vigilance Test (PVT; Roach, Dawson, & Lamond, 2006). Also the day's mood was assessed using the Positive And Negative Affect Scale (PANAS, Watson, Clark, & Tellegen, 1988).

Study 2 followed the same procedure. However, it focussed on the early SWS-rich sleep interval only.

2.3. Memory task

2.3.1. Materials

For the picture learning task, four-hundred pictures were selected from the International Affective Picture System (IAPS; Lang, Greenwald, Bradley, & Hamm, 1993) and divided into two parallel sets of 48 low arousing neutral and 48 medium to high arousing negative pictures (for the subjects' two conditions), respectively. To enable two recall tests, i.e., immediate recall testing (baseline) during the learning phase and delayed recall testing during the retrieval phase, each of these sets was again subdivided into two parallel sets each containing 24 neutral and 24 emotional pictures; and these sets were each supplemented with 24 new pictures. Normative valence (scale from negative [1], neutral [5] to positive [9]) and arousal (scale from not arousing at all [1] to very arousing [9]) ratings were comparable for the eight sets (all $p > 0.99$): [mean ± SD across all sets] valence ratings: negative, 3.11 ± 1.60; neutral, 5.01 ± 1.22; arousal ratings: negative,