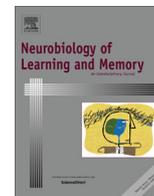




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Replay of conditioned stimuli during late REM and stage N2 sleep influences affective tone rather than emotional memory strength

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ABSTRACT

Emotional memories are reprocessed during sleep, and it is widely assumed that this reprocessing occurs mainly during rapid eye movement (REM) sleep. In support for this notion, vivid emotional dreams occur mainly during REM sleep, and several studies have reported emotional memory enhancement to be associated with REM sleep or REM sleep-related parameters. However, it is still unknown whether reactivation of emotional memories during REM sleep strengthens emotional memories. Here, we tested whether re-presentation of emotionally learned stimuli during REM sleep enhances emotional memory. In a split-night design, participants underwent Pavlovian conditioning after the first half of the night. Neutral sounds served as conditioned stimuli (CS) and were either paired with a negative odor (CS+) or an odorless vehicle (CS−). During sound replay in subsequent late REM or N2 sleep, half of the CS+ and half of the CS− were presented again. In contrast to our hypothesis, replay during sleep did not affect emotional memory as measured by the differentiation between CS+ and CS− in expectancy, arousal and valence ratings. However, replay unspecifically decreased subjective arousal ratings of both emotional and neutral sounds and increased positive valence ratings also for both CS+ and CS− sounds, respectively. These effects were slightly more pronounced for replay during REM sleep. Our results suggest that re-exposure to previously conditioned stimuli during late sleep does not affect emotional memory strength, but rather influences the affective tone of both emotional and neutral memories.

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1. Introduction

Emotional events undergo preferential memory consolidation compared with neutral events (Cahill & McGaugh, 1998; McGaugh, 2006). In a laboratory setting, emotional learning is usually investigated with Pavlovian conditioning (Pavlov, 1927). In this procedure, an initially neutral conditioned stimulus (CS) is repeatedly presented with an aversive unconditioned stimulus (UCS). Importantly, different time contingencies between the CS and the UCS involve different brain structures: learning the association by trace conditioning with a time delay after the offset of the CS and the onset of the UCS is hippocampus-dependent (Solomon,

Vander Schaaf, Thompson, & Weisz, 1986), whereas delay conditioning with an overlapping presentation of the UCS at the end of the CS presentation relies mostly on the amygdala (Fanselow & LeDoux, 1999; Maren, 2001).

Sleep is assumed to play an important role in emotional memory re-processing (Hu, Stylos-Allan, & Walker, 2006; Wagner, Gais, & Born, 2001; for a review see Payne & Kensinger, 2010). In particular, it is widely assumed that rapid eye movement (REM) sleep, earlier termed as dream sleep, is critically involved in this process. Possibly related to the notion that vivid and emotional dreams mostly occur after awakening from REM sleep (Hobson, Pace-Schott, & Stickgold, 2000), many psychoanalytic approaches assume that dream sleep-related dreams are critically related to reprocessing of previously encountered emotional events (Freud, 1900). In addition, a high number of studies in rodents using emotional learning tasks like Pavlovian conditioning or active avoidance tasks have revealed strong evidence for a role of REM sleep in emotional memory consolidation: In these studies, REM sleep increases are frequently observed after learning during specific

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time windows and correlated with learning success, while suppressing REM during these times impaired learning (Smith, 1985, 1996 for reviews and meta-analyses). As a possible underlying mechanism, ponto-geniculo-occipital waves occurring during REM sleep as well as reactivations on the amygdala and hippocampus level have been proposed (Datta & O'Malley, 2013; Hennevin, Huetz, & Edeline, 2007). In fact, in rodents, patterns of hippocampal memory reactivation have been observed during REM sleep (Louie & Wilson, 2001; Poe, Nitz, McNaughton, & Barnes, 2000), and presentations of memory cues during REM sleep activate hippocampal neurons (Maho & Bloch, 1992) and increase avoidance responses to previously conditioned stimuli (Hars, Hennevin, & Pasques, 1985).

In addition to the strong evidence for the role of REM sleep in the consolidation of emotional memories in rodents, also human studies provide support for this notion. For example in split-night paradigms, emotional memory for pictures and stories was particularly enhanced after a period of late, REM sleep-rich sleep, but not after periods of early slow-wave sleep (SWS)-rich sleep (Groch, Wilhelm, Diekelmann, & Born, 2013; Wagner, Fischer, & Born, 2002; Wagner et al., 2001). Furthermore, the deprivation of REM sleep led to less emotional-laden memory of stories (Greenberg, Pearlman, Schwartz, & Grossman, 1983) and changes in REM sleep are often involved in disorders affecting emotional processing (Tsuno, Besset, & Ritchie, 2005). In addition, several studies have reported positive correlations with REM sleep-related parameters and memory for emotional information (Baran, Pace-Schott, Ericson, & Spencer, 2012; Menz et al., 2013; Nishida, Pearsall, Buckner, & Walker, 2009; Payne, Chambers, & Kensinger, 2012). According to a recent theoretical account, emotional memories are reactivated during REM sleep by covert amygdaloid reactivations, causing a strengthening of the declarative, informational content of the memory and a decrease of the emotional reactivity to this memory (Van der Helm et al., 2011; Walker & van der Helm, 2009, although see Baran et al., 2012; see Rasch & Born, 2013 for a review).

While an association between REM sleep and emotional memory appears to be well-established in rodents, experimental evidence for a critical role of emotional memory reactivation during REM sleep for consolidation processes is still scarce in humans. Induced memory reactivation during REM sleep has been shown to improve performance in complex logical tasks (Smith & Weeden, 1990) as well as generalization of sound-face associations (Sterpenich et al., 2014), while no behavioral effects of targeted memory reactivation with respect to the emotionality of the associated faces (i.e., negative vs. neutral) were reported in the latter study. For neutral declarative memory tasks, targeted memory reactivation during REM sleep is ineffective (Cordi, Diekelmann, Born, & Rasch, 2014; Rasch, Büchel, Gais, & Born, 2007). In fact, recent studies revealed evidence that emotional memories could be influenced by reactivation in SWS during midday naps (Cairney, Durrant, Hulleman, & Lewis, 2014; Hauner, Howard, Zelano, & Gottfried, 2013), but these studies did not include a REM sleep condition. Thus, it still remains an open question if re-exposure to emotional memories during REM sleep can affect emotional memory performance after sleep in humans.

To test this question, we used a between-subject, split-night design where participants slept during the first half of the night, were awoken to undergo hippocampus-independent Pavlovian delay conditioning after the first half and slept again during the second half. During conditioning learning, half of the neutral sounds were associated with a negative odor (UCS) and the other half with an odorless vehicle, resulting in CS+ (sounds followed by the odor) and CS- (sounds followed by the odorless vehicle). During subsequent sleep in the second half of the night, half of the sounds that were previously learned as negative (CS+) and half

of the sounds that were previously learned as neutral (CS-) were replayed without the odor or the odorless vehicle, respectively. The target sleep stages for sound re-presentation differed between two groups – REM sleep or N2 sleep as control. Recall took place 36 h later, after a recovery night. We hypothesized that replay of the CS+ during REM sleep will result in enhanced memory for this association compared with replay during N2 sleep, expressed in higher odor expectancy, higher physiological reactivity, and higher subjective affective reactivity.

2. Materials and methods

2.1. Participants

Thirty-five healthy, non-smoking women naïve to the experimental protocol participated in the study. Participants were randomly assigned to two groups, depending on the sleep stage during which replay took place: “REM sleep replay group” ($N = 19$) and “N2 sleep replay group” ($N = 16$). As exclusion criterion, we defined a difference value between all CS+ and all CS- over the whole course of learning (80 trials total) of 0.5. Based on this differentiation score, data from five subjects had to be excluded. This resulted in 30 participants included in the final analysis (REM replay group: $N = 16$, N2 replay group: $N = 14$). Age distribution was highly comparable between sleep replay groups (mean age: 23.30 ± 2.72 years (SD); range: 18–32 years; $t(28) = 0.291$, $p > 0.70$). Participants were in good physical and mental health according to a routine examination: They did not take any psychologically active medication at the time of and one month prior to the experiment, and reported a normal sleep-wake cycle. They had not been on night shift, did not experience long distance flights, did not have any major sleep disturbances during eight weeks prior to the experiment, and had a good sleep quality according to the Pittsburgh Sleep Quality Index (PSQI; Buysse, Reynolds, Monk, Berman, & Kupfer, 1989) (mean PSQI score: 3.50 ± 0.28 ; no differences between groups: $t(28) = -0.94$, $p > 0.30$). They had normal olfactory and auditory functions. Any nasal infections were excluded on the day of the experiment. Participants underwent a UCS test during which they had to rate the valence of the odor used for aversive conditioning and another odor as distractor on a 9-point scale (1–3 negative, 4–6 neutral, 7–9 positive). They were only included if they rated the UCS odor as negative (mean rating: 2.24 ± 0.77 ; no significant group difference: $t(28) = 0.53$, $p > 0.50$). On the experimental day, general olfactory performance was tested using the “Sniffin’ Sticks” inventory (Burghart, Germany). The general ability to distinguish between twelve odors (mean: 11.10 ± 0.15) and olfactory thresholds (mean: 5.52 ± 0.35) was comparable between groups (both $p > 0.30$). At the beginning of the main experiment, subjects received the information that the learning task during the night will consist of odors and sounds and that some sounds will be presented also during sleep at a volume which will not disturb their sleep. Subjects were habituated to the experimental setting by spending an adaptation night in the sleep laboratory under experimental conditions. On experimental days, participants were instructed to get up at 7.00 a.m., not to take any naps and not to ingest alcohol or, after 3.00 p.m., caffeine-containing drinks. All subjects gave written informed consent prior to participation and received monetary compensation after the last session. The experiment was approved by the Cantonal Ethics Commission of Zurich.

2.2. Design and procedure

At least two days after fulfilling the UCS odor rating and the adaptation night, participants underwent the emotional learning

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