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Modulating influences of memory strength and sensitivity of the retrieval test on the detectability of the sleep consolidation effect

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ABSTRACT

Emotionality can increase recall probability of memories as emotional information is highly relevant for future adaptive behavior. It has been proposed that memory processes acting during sleep selectively promote the consolidation of emotional memories, so that neutral memories no longer profit from sleep consolidation after learning. This appears as a selective effect of sleep for emotional memories. However, other factors contribute to the appearance of a consolidation benefit and influence this interpretation. Here we show that the strength of the memory trace before sleep and the sensitivity of the retrieval test after sleep are critical factors contributing to the detection of the benefit of sleep on memory for emotional and neutral stimuli.

228 subjects learned emotional and neutral pictures and completed a free recall after a 12-h retention interval of either sleep or wakefulness. We manipulated memory strength by including an immediate retrieval test before the retention interval in half of the participants. In addition, we varied the sensitivity of the retrieval test by including an interference learning task before retrieval testing in half of the participants. We show that a "selective" benefit of sleep for emotional memories only occurs in the condition with high memory strength. Furthermore, this "selective" benefit disappeared when we controlled for the memory strength before the retention interval and used a highly sensitive retrieval test. Our results indicate that although sleep benefits are more robust for emotional memories, neutral memories similarly profit from sleep after learning when more sensitive indicators are used. We conclude that whether sleep benefits on memory appear depends on several factors, including emotion, memory strength and sensitivity of the retrieval test.

1. Introduction

Emotion is important for the encoding and consolidation of memories. Numerous studies have shown that emotional content is remembered better than neutral content for words (e.g. Adelman & Estes, 2013; Kensinger & Corkin, 2003), stories (e.g. Cahill & McGaugh, 1995; Heuer & Reisberg, 1990) and pictures (e.g. Blake, Varnhagen, & Parent, 2001; Harris & Pashler, 2005). The strengthening effect of emotion on memory is linked to the activation of emotion-related brain regions including the amygdala, which modulates encoding and consolidation of memories in the hippocampus (e.g. Canli, Zhao, Brewer, Gabrieli, & Cahill, 2000; Phelps, 2004).

In addition to emotion, sleep also fosters memory consolidation after learning. Numerous studies have provided compelling evidence that sleep occurring shortly after learning results in an improvement of later memory retrieval performance as compared to a retention interval filled with wakefulness (see Rasch & Born, 2013 for a comprehensive review). Importantly, sleep's role in memory is considered active: According to the active system consolidation hypothesis, recently learned memories are spontaneously reactivated during sleep and thereby stabilized and integrated into neocortical memory networks for long-term storage. This system consolidation critically depends on several sleep-specific oscillatory brain signals, including hippocampal sharp-wave ripples, sleep spindles and slow-oscillations (Born & Wilhelm, 2012). Thus, according to this notion, sleep is not passively providing a shelter for temporary memory maintenance, but actively supports consolidation processes.

One important additional assumption in support of an active role of sleep for memory is that consolidation processes during sleep are selective (e.g. Rasch & Born, 2013; Stickgold & Walker, 2013). For example, it is assumed that sleep selectively consolidates memories that are relevant for the future, including emotional memories and memories associated with a reward. Regarding the selective consolidation of emotional memory content Hu, Stylos-Allan, and Walker (2006)

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showed that sleep after learning enhanced recognition performance only for emotional but not neutral images. Along similar lines, Payne and colleagues showed that a full night's sleep (Payne, Stickgold, Swanberg, & Kensinger, 2008) but also a brief nap (Payne et al., 2015) enhanced the recognition of central emotional objects in a scene, but not central neutral objects or the neutral backgrounds of that scene. Furthermore, Wagner, Gais, and Born (2001) reported that only emotional texts benefited from three hours of REM-rich sleep, but neutral texts did not.

Interestingly, in these studies the selective benefit of sleep for emotional memories is typically accompanied by a reduced or absent benefit of sleep for neutral memories. This is a puzzling finding, as numerous studies have consistently observed a sleep benefit for memory when using only neutral learning materials, including words, word-pairs and even senseless syllables (e.g. Jenkins & Dallenbach, 1924; Plihal & Born, 1997). Payne et al. (2008) have explained this paradox by arguing that when both emotional and neutral stimuli are presented together, a "trade-off" mechanism preferentially consolidates the emotional stimuli, as they are biologically more relevant. Bennion, Payne, and Kensinger (2015) suggest an early "emotional tagging" mechanism as a basis for this trade-off which selects memories for preferential consolidation. This could lead to a sleep-dependent alteration of brain activation as Payne and Kensinger (2011) report a strengthened connection between the amygdala, the hippocampus and the ventromedial prefrontal cortex during retrieval of emotional, but not neutral content after sleep compared to wakefulness.

However, not all studies find a prioritized consolidation of emotional items over neutral ones (Baran, Pace-Schott, Ericson, & Spencer, 2012; Lehmann, Seifritz, & Rasch, 2016; Lewis, Cairney, Manning, & Critchley, 2011). Baran et al. (2012) explain these divergent findings by highlighting the different experimental designs used across studies including variation of stimuli, range of emotional variance and presentation times. Bennion et al. (2015) discuss that besides the emotionality of the content, there are other important factors for the tagging mechanism such as stimulus novelty, state of the individual experiencing the event and neurochemical processes accompanying the emotional reaction.

Apart from methodological issues and tagging, an alternative explanation is that the benefit of sleep for memory is rather dependent on the strength of memory traces before sleep. Emotional memories are typically remembered better than neutral ones already during immediate recall attempts. Thus, sleep might simply require a certain threshold of memory strength during encoding to ensure that consolidation mechanisms during sleep can stabilize and integrate these new memories into long-term storage. One could argue that in some previous studies, emotional memories – which are more strongly encoded before sleep – pass the threshold for being consolidated during sleep, while weaker neutral memories do not. In contrast, when neutral material is repeatedly learned or studied until a certain criterion (e.g. 60%), a sleep benefit is observed also for solely neutral learning material (see e.g. Drosopoulos, Schulze, Fischer, & Born, 2007). Please note that the same study also reported that learning to a very high criterion (i.e., 90%) abolishes the beneficial effect of sleep on memory. This pattern of results suggests that the benefit of sleep on memory might be maximal at medium memory strengths, with lower or no effects for very weakly or very intensively encoded memories.

One possible way to increase memory strength in studies using emotional and neutral learning material is inserting an immediate retrieval right before the retention interval. Implementation of immediate recall of memories before the retention period should enhance the accessibility of these memories through a mechanism of effortful processing (Rowland, 2014), a phenomenon known as the testing effect (Sutterer & Awh, 2015). Thus, if the benefit of sleep relies on memory strength, we would expect that the neutral memories also benefit from sleep when their memory strength is enhanced due to immediate retrieval testing. This testing right after learning also enhances memory strength by changing the expectancy of the future relevance of this memory (Wilhelm et al., 2011), as subject's attention might be shifted towards the memory aspect of the task in contrast to the conditions without immediate recall. This offers the opportunity for an intentional reconsolidation after learning to the advantage of memory strength.

Another explanation for the divergent findings in the literature might be the sensitivity of the retrieval test. Several studies in this field used recognition measures, although very few studies have successfully observed sleep benefits on recognition using different kinds of learning material (see Diekelmann, Wilhelm, & Born, 2009). The authors of the review concluded that cued or free recall tests detect sleep benefits much more reliably than recognition tests (Diekelmann et al., 2009). While the reasons are still unclear, one might argue that sleep mostly facilitates retrieval access by reactivating memories during sleep which is less relevant for recognition, particularly with respect to familiarity judgements. Another possible reason is that recognition performance is typically very high, which might be less ideal to successfully detect sleep-benefits on memory. To increase the sensitivity of retrieval testing even further, an interference learning block can be inserted before the retrieval task. For example, Ellenbogen, Hulbert, Stickgold, Dinges, and Thompson-Schill (2006) showed that interference before retrieval testing resulted in a larger benefit of sleep for memory of neutral word-pairs. These findings were replicated even when controlling for circadian factors and using a more refined behavioral paradigm (Ellenbogen, Hulbert, Jiang, & Stickgold, 2009), as well as in both younger and older adults (Sonni & Spencer, 2015). However, some divergent findings have also been reported, where interference reduced or nullified the sleep benefit (Barsky, Tucker, & Stickgold, 2015; Deliens et al., 2013), though the interference paradigm used in Deliens et al. (2013) was based on emotional interference rather than interference of another learning set. Thus, if the observation of the benefits of sleep on memory depends on the sensitivity of the retrieval testing, it might be possible to reveal sleep benefits on neutral memories even in the presence of emotional memories by inserting interference before retrieval testing.

Here we tested these two possibilities by systematically varying memory strength and the sensitivity of the retrieval testing. Participants viewed emotional and neutral pictures and freely recalled them after a 12-h retention interval filled with either sleep or wakefulness (see Fig. 1 for overview of the task design and experimental procedure). Half of the participants immediately recalled the pictures additionally before the interval, and the other half did not. Furthermore, half of the participants performed interference learning before free recall testing after the retention interval and the other half did not. We hypothesize that the appearance of the beneficial effect of sleep depends on both the memory strength and the sensitivity of the retrieval testing. Thus, we expect to observe a selective effect of sleep for emotional memories only when the memory strength of neutral memories is low (i.e. without immediate retrieval testing). In addition, we expect that the observed selectivity of sleep for emotional memories will disappear when the sensitivity of the retrieval test is increased (i.e. with interference learning before retrieval).

2. Materials and methods

2.1. Participants

In total, 235 healthy subjects (158 female, mean age ± SD = 24.42 ± 4.11) participated in the experiment. Seven subjects were excluded from analysis due to non-compliance with either task instruction (n = 1) or study protocol (n = 3), technical difficulties (n = 1) or being an outlier in the memory task (> 3 standard deviations of the overall mean; n = 2). This left a total of 228 subjects between 18 and 35 distributed across four experimental groups, each split into a sleep and a wake condition (see Fig. 1). Participant characteristics for each experimental group are reported in Table 1. Group IV has previously been reported as the pilot study in Ackermann, Hartmann,