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Golden slumber?

The elusive role of sleep in emotional memory

Reinhold, F.L.

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Chapter 1

General introduction

"In her sleep is the place of remembering. It is the place where there is no pretense."

– bell hooks

"I've been told that the insomnia I've struggled with on and off for most of my life comes from drinking too much caffeine or eating too much sugar or sleeping on a bed that's too soft or too hard or too flat. That I don't exercise enough or that I exercise too much. Or that I exercise the right amount, but at the wrong time of day. Or that it's the result of watching TV or using a computer right before I go to bed. Though isn't that when everyone pokes around on the computer or watches TV? [...] What my insomnia is really about is being afraid. [...] Being afraid when I was a kid." – "And I'd lie awake at night, scared to fall asleep, because sleep seemed no different than death. [...] You are gone, not moving, not talking, not thinking, not aware – *not aware*. [...] There is a lot to fear. [...] This altered state where we're vulnerable and just gone." (Glass, 2008)

The death of a loved one can transform the most routine parts of our lives – even something as ordinary as falling asleep, especially for a child still learning what it means to be gone but not gone forever. But also as adults we are sometimes afraid of entering this vulnerable state, haunted, night after night, by recurring nightmares. Nightmares of what we may fear, or of what once was, or still is, our reality. Whether rooted in imagination or memory, our experiences during sleep often mirror the emotional traces of our past. Alongside the moments we cherish – a kind word from a stranger, uncontrollable laughter with close friends, or the sense of freedom on a long road trip – our lives are also marked by difficult ones. Memories we sometimes still try to forget. From childhood arguments between parents, to adolescent feelings of not fitting in, to adult grief of losing someone close. And while these moments, both joyful and painful, shape who we are today and help us navigate through life, it is often the painful ones that can also overwhelm us, leaving us challenged, helpless, and at times, even follow us into our sleep.

The emotional moments that persist in our minds as mental representations are referred to as *emotional memories* (for review, see Arntz, 2020; Freund et al., 2022). These memories play a central role in shaping our perceptions, beliefs, and expectations about ourselves, others, and the world, thereby guiding future decisions and behaviours. For instance, after experiencing a bike accident, we may change our perception of how safe cycling is, leading us to become more vigilant when cycling to reduce the risk of future incidents. This example illustrates the broader understanding of learning and memory as an adaptive function: even simple organisms rely on the ability to access information from past

experiences, enabling them to adjust their behaviour to an ever-changing environment, increasing their chances of survival (Dussutour, 2021; McGaugh, 2000). Yet, that same bike accident might also evoke intense fear, causing us to perceive cycling as overly dangerous and avoid it altogether, even if the actual risk of another accident is low (unless you live in Amsterdam). When persistent, such memories may contribute to the development of psychological symptoms. Indeed, emotional memories often underlie the onset and maintenance of many affective disorders, such as anxiety disorders, depression, addiction, and post-traumatic stress disorder (Kindt, 2014; Mineka & Zinbarg, 2006). Numerous epidemiological studies have shown that disorders rooted in emotional memory rank among the most common and debilitating chronic conditions in both Europe (Wittchen & Jacobi, 2005) and the United States (Kessler et al., 2005). The substantial burden these disorders place on individuals and society, combined with growing global exposure to traumatic events such as war and climate-related disasters (due to inadequate political actions), underscores the urgent need for more effective prevention and treatment options. We thus set out to answer the question: can we change the impact emotional memories have on us?

To answer this, we first need to understand how emotional events are actually stored. Like all recently acquired, or encoded, information, emotional experiences form a new memory trace that initially remains in a labile state (McGaugh, 2000). To become stable, this memory trace must undergo *consolidation* – a process that not only strengthens the memory but also integrates it into existing memory networks for long-term storage (e.g., Dudai et al., 2015). However, when an emotional experience evokes intense emotional reactions, consolidation has been suggested to be disrupted or incomplete (e.g., Brewin et al., 1996; Ehlers & Clark, 2000; but see e.g., Cahill & Alkire, 2003), causing the resulting memories to influence our thoughts and behaviours in maladaptive ways. For example, following the bike accident, poorly integrated emotional memories might manifest as flashbacks or distressing intrusive thoughts of scenes of the accident, easily triggered by seemingly unrelated cues. Disrupted consolidation can also contribute to ruminative thinking, such as persistent worry about future accidents. Importantly, these disturbances are not limited to cognitive processes – they can also be expressed behaviourally, for instance, through avoidance of cycling or hypervigilance in traffic. If excessive emotions resulting from disrupted consolidation play a role in the development and persistence of psychological disorders, then targeting the emotional intensity associated with the original event – by dampening it early or modifying it later – may support prevention and treatment, respectively. Thus,

identifying factors that facilitate emotional memory processing is crucial, and one such factor has been suggested to be *sleep*.

Much like learning and memory, sleep serves an adaptive function essential to the survival of many species, as shown by decades of research (Foster, 1901; Mader & Mader, 2016; Siegel, 2005). Every night, we cycle through multiple stages of sleep, each supporting vital functions such as immune regulation (Ibarra-Coronado et al., 2015), cognitive performance (Goel et al., 2009; Richards et al., 2017), and emotion regulation (Gruber & Cassoff, 2014). In contrast, sleep disturbances or deprivation can compromise both our physical and mental health. Animal studies show that prolonged sleep deprivation can cause fatal infections and tissue damage (Rechtschaffen & Bergmann, 1995), while human studies additionally report severe emotional impairments (Brown, 2012; Fiorino, 1996; Vandekerckhove & Cluydts, 2010). In fact, sleep disturbances often co-occur in a broad range of affective disorders (Freeman et al., 2020; Ohayon & Roth, 2003; Stepanski & Rybarczyk, 2006), and growing evidence indicates that such disturbances do not only result from psychopathology but also contribute to the development and maintenance of symptoms (Harvey, 2008; Talamini et al., 2013), pointing at a bidirectional link between sleep and affect. It is often when sleep is disrupted that things begin to unravel.

Beyond its impact on emotional well-being, poor sleep has been consistently linked to deficits in cognitive functioning (Killgore, 2010), particularly in memory-related processes (Diekelmann & Born, 2010; Goel et al., 2009; Walker & Stickgold, 2006; Yoo et al., 2007). In contrast, healthy sleep appears to facilitate learning and memory. Extensive research indicates that sleep plays a key role in preparing the brain to effectively encode new information, as well as stabilizing, reorganizing, and transferring memories from short-term (e.g., hippocampus) to long-term storage (e.g., neocortex), thereby enhancing later access to those memories (Alger et al., 2015; Diekelmann & Born, 2010; Payne, 2011; Payne, Ellenbogen, et al., 2008; Payne, Stickgold, et al., 2008; Stickgold & Walker, 2013). Thus, sleep seems to not only passively protect memory traces of recently acquired information by reducing sensory input and cognitive demands typically present during wakefulness, but also actively contributes to their consolidation.

Given the brain's limited capacity to process and store the vast amount of information we encounter each day, a question that remains unanswered is whether it uses mechanisms to selectively tag certain information as important to remember while allowing others to be forgotten. Emotionally charged information, especially that which may signal threat or reward, is thought to be prioritized in memory as an adaptive function. Evidence suggests

that sleep contributes to this process by selectively strengthening emotionally salient memories (for review, see Lipinska et al., 2019), indicating that sleep likely supports selective consolidation, eliminating trivial information while integrating useful material (Ambrosini et al., 1988; Giuditta, 2014). We initially set out to further investigate this selective consolidation process, focusing on how sleep might downscale irrelevant information as an underlying mechanism of a promising treatment approach for emotional memory disorders. While it was once widely believed that consolidated memories are fixed and unchangeable, groundbreaking research in animals has shown that retrieving a memory can return it to a malleable, or labile, state, opening a window in which the memory can be modified before it is *reconsolidated* (Nader et al., 2000; Sara, 2000). Subsequent studies in humans have provided supporting evidence for this mechanism, suggesting that it may be possible to selectively attenuate the affective component of a previously consolidated emotional memory through pharmacologically induced amnesia without erasing the memory of the event itself (Craske et al., 2014; Dudai & Eisenberg, 2004; Kindt et al., 2009; Sevenster et al., 2012b, 2013; Soeter & Kindt, 2010, 2012b, 2012a, 2015). Returning to the bike accident example: if the fear associated with the memory of the accident is so strong that it leads us to completely avoid cycling, then reducing that fear response could allow us to resume our daily commuting habits. Curiously, sleep seemed to be essential to successfully restabilize the modified memory, though the exact mechanism is still unclear. Hence, our original goal of this dissertation was to explore how sleep aids in the reconsolidation of emotional memories. A commonly used paradigm to study the malleability of associative fear memories in the laboratory is Pavlovian conditioning, which is thought to model the associative fear learning processes underlying anxiety disorders (Grillon, 2008). In this paradigm, a neutral stimulus becomes feared (e.g., an image of a bicycle) because it predicts a negative or aversive outcome (e.g., an electric shock). Once this association is formed (i.e., consolidated), it becomes possible to modify the fear response triggered by exposure to the feared stimulus. Despite a series of pilot studies conducted over several years, we were, however, unable to reliably induce fear memories using Pavlovian conditioning, as reflected in startle responses (our primary outcome measure). Therefore, testing subsequent changes in fear memory was not feasible.

Gradually accepting defeat, we shifted our focus from experiments seeking insights into how emotional memory disorders might be treated to experiments exploring how they could be prevented. Considering the bike accident did not cause any major physical injuries, the adrenaline still rushes through our veins and the shock sits deeply. In moments like these,

we often turn to friends or family members for comfort, who might say something like “Just take a deep breath – you’ll feel better about it tomorrow.” This reassuring phrase implies that a good night of sleep can weaken the emotional impact the experience has on us. Simply put, should we just go to sleep after experiencing a bike accident? What appears to challenge this assumption is the earlier evidence indicating that sleep selectively strengthens emotional memories (Lipinska et al., 2019). However, these studies primarily focused on how well we remember the content of emotional material, not what happens to the emotional intensity tied to those memories. Building on this distinction, two competing hypotheses have emerged. Both align in their view that sleep enhances the factual elements of emotional memories (e.g., when and where the bike accident happened), yet they diverge in how sleep modulates the affective *tone* of those memories (i.e., how the event makes us feel).

The “emotional salience consolidation” account posits that sleep preserves, or even enhances, not only the content but also the emotional intensity that was experienced during a certain event (Baran et al., 2012; Pace-Schott et al., 2011; Wagner et al., 2002; Werner et al., 2015). This hypothesis is supported by evidence showing that during rapid eye movement (REM) sleep – a prominent stage of the sleep cycle – brain regions associated with emotional processing are highly active (Maquet et al., 1996). This heightened activity is assumed to facilitate the reactivation and strengthening of emotionally charged memory traces. If this hypothesis holds, maintaining or amplifying memories’ emotional intensity during sleep could prolong or intensify the emotional impact they have on us. Thus, sleeping after experiencing a bike accident may actually *not* help us feel better.

In contrast, the “sleep to forget and sleep to remember” hypothesis suggests that sleep serves a dual role by reducing the emotional intensity of memories (“sleep to forget”) while maintaining their episodic details (“sleep to remember”; Walker & van der Helm, 2009). While this theory aligns with the idea that REM sleep facilitates the reactivation of emotional memory traces via heightened activity in emotion-related brain regions, it further emphasizes that this reactivation occurs in a neurochemical environment characterized by a low noradrenergic tone. The reduction in noradrenaline release is suggested to be due to the suppression of locus coeruleus (LC) activity during REM sleep, sometimes referred to as LC silencing (Aston-Jones & Bloom, 1981a, 1981b; Swift et al., 2018). As a result, emotional memories may be consolidated in the absence of elevated physiological arousal, leading to a diminished autonomic response when the memory is later retrieved. If the decoupling between memory content and emotional intensity is not fully achieved during the first night of sleep following the event, this process is thought to continue across subsequent nights,

as the memory remains tagged as salient or “important” until its emotional component has been sufficiently downregulated. According to this model, sleep may reduce the emotional impact of distressing experiences by mitigating their affective tone. As such, sleeping after the bike accident could indeed help us to feel better when remembering it.

Although a growing body of research has explored sleep’s impact on the emotional tone of memories, their findings have been inconsistent (for reviews, see Davidson & Pace-Schott, 2021; Tempesta et al., 2018). Some evidence supports the “emotional salience consolidation” account, demonstrating that sleep preserves or enhances the emotional intensity of memories. Other outcomes align with the “sleep to forget and sleep to remember” hypothesis, linking sleep to the attenuation of the affective tone. Yet a number of studies also report no effect of sleep at all. As a result, literature reviews have concluded that no consistent pattern has emerged regarding sleep’s modulatory role, which has been attributed to methodological differences across studies, including variations in experimental design, the operationalisation of emotional memories, the type of emotional response measured (e.g., subjective ratings versus physiological indicators), and the analytical methods used. Thus, we set out to resolve the conflicting evidence, still hopeful that we might settle the question of whether we can change the impact of emotional memories have on us by sleeping. Rather than relying on typical laboratory approaches, such as associating an image of a bicycle with an uncomfortable (but not yet painful) electric shock, we adopted more naturalistic experimental paradigms. By asking participants to sing, solve math problems, and give unprepared presentations to create painfully embarrassing memories, we systematically investigated whether, and under what conditions, sleep modulates their emotional intensity.

Outline of the dissertation

Methodological variability in previous research has been suggested to underly the ongoing inconsistencies in the field (Davidson & Pace-Schott, 2021). For example, many studies failed to include proper control stimuli to isolate memory-specific from more general changes in affect. In addition, emotional memories were often induced using negatively valenced images, which may fail to evoke strong emotional responses and/or personally meaningful events. In this dissertation, we address these limitations by introducing more ecologically valid, well-controlled paradigms to examine sleep’s modulatory effect on the emotional tone of memories. Accordingly, in the first two studies, we moved beyond the conventional approach of using negatively valenced images by employing a karaoke paradigm to create

naturally embarrassing autobiographical experiences. Participants were first recorded singing two different songs, after which one of the recordings was played back to induce an embarrassing episode. In **Chapter 2**, participants were re-exposed to the original recording as well as to a newly presented one (i.e., control stimulus), following a 12-hr interval that included either nighttime sleep or daytime wakefulness. This design allowed us to distinguish memory-specific emotional responses from general emotional reactivity, offering insight into whether a single night of sleep alters the emotional tone associated with the reactivation of emotionally salient experiences. In **Chapter 3**, we examined the possibility that sleep-related emotional modulation may require more than one night of sleep and benefits when the interval of wakefulness between an emotional experience and the first sleep opportunity is shorter. While most prior studies have focused on single-night effects, we extended this approach by examining whether immediate, compared to delayed, post-encoding sleep modulates the emotional intensity of a memory reactivated one week later.

Given that the findings from those two studies did not yield a clear conclusion about whether sleep alters the affective tone of emotional memories, we considered the possibility that additional factors may shape the direction of this effect (Genzel et al., 2015; Hutchison & Rathore, 2015). Rather than assuming that sleep uniformly weakens or strengthens the emotional tone, the effect may vary according to what is most adaptive. Thus, in **Chapter 4**, we investigated whether the perceived future relevance of an emotional experience influences how sleep modulates its emotional intensity. We reasoned that maintaining the emotional tone of *future-relevant* memories could serve an adaptive function by helping individuals better prepare for similar situations, whereas the emotional tone of *future-irrelevant* memories should be downregulated to minimize unnecessary emotional load. To examine this, we developed a novel evaluative learning paradigm using a short film clip depicting an acted version of the Trier Social Stress Test (TSST; Kirschbaum et al., 1993). Some of the actors portraying either a critical or neutral evaluation panel member were later introduced as members of the panel evaluating the participant's own presentation one week later, thereby assigning future relevance or irrelevance to the learned associations. Changes in the emotional tone were assessed both after a 12-hr interval containing either daytime wakefulness or nighttime sleep, and again one week later. This approach allowed us to examine whether the effect of sleep on the emotional tone is influenced by the anticipated future significance of the associated memory.

Since no convincing sleep-related changes in the emotional tone of memories were observed, even when accounting for factors such as future relevance, **Chapter 5** addresses

a potential limitation of how emotional memories were reactivated in prior work (including our own). Re-exposing participants to negative stimuli may confound memory retrieval with the emotional response to re-experiencing the stimulus itself. Therefore, we aimed to better isolate pure memory retrieval while also assessing a more ecologically valid measure of emotional memory by examining the effect of sleep on spontaneous recall in the form of intrusive memories, which are considered markers of incomplete or impaired emotional memory processing (e.g., Brewin et al., 1996; Ehlers & Clark, 2000). To elicit intrusive memories, we induced a distressing experience using a modified version of the Trier Social Stress Test as part of the study described in **Chapter 4**, which involved an arithmetic task and a minimally prepared speech delivered in front of a critical panel. Over the following week, participants documented any related intrusive memories and rated their associated distress. To more comprehensively capture sleep's effect on their disruptive impact, we combined both frequency and distress of intrusive memories in a composite measure (Rattel et al., 2019, 2022). This approach could provide a more integrated test of the two leading hypotheses by examining not only how sleep modulates the emotional intensity of distressing experiences – reflecting changes in the affective tone of memories – but also how it influences memory retention, as the frequency in intrusive memories may indicate potential impairments in memory integration.

In the final chapter (**Chapter 6**), we discuss the theoretical and clinical implications of our findings, reflecting on how they advance our understanding of sleep's role in modulating the emotional impact of memories. We also address remaining challenges and limitations in the field that may hinder progress and suggest directions for future research to better unravel the complex relationship between sleep and emotional memory processing.