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Chapter 28

SLEEP, MEMORY AND EMOTIONS

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EMOTIONS, MEMORY AND SLEEP

Every day we learn. The question is how can we memorize and sort out the relevant bits of the vast amounts of information encountered each day. Today it is believed that sleep and "offline consolidation" do play a crucial role in this process (cf. Dang-Vu, Schabus et al. 2010). Consolidation is a process occurring as soon as fresh information has been encoded by the brain. It depends on the brain's plasticity that is the function to form new memories and integrate that new information into long-term memory according to subjective needs at a neuronal level. From everyday experience we know that emotional content has some advantage when it comes to forming a memory with specific "offline" benefits overnight. On average, people can remember almost twice as much of text when it is emotionally charged as compared to neutral information (Wagner, Degirmenci et al. 2005). The growing number of studies on sleep-dependent memory consolidation both confirm the benefits of various memory systems from specific sleep stages or sleep patterns but also reveal accumulating discrepancies and open issues (Schabus 2009). At the end, the success story of sleep and memory appears much less straightforward than originally believed.

The Role of Sleep for Emotional Memory

It has been reported that after a full-night sleep, in comparison to control day-time wakefulness, accuracy (d') in emotional picture recognition is improved (Hu, Stylos-Allan et al. 2006). In addition, Lewis and colleagues reported better declarative contextual memory performance after sleep compared to wakefulness, but in the same order for emotional and neutral material (Lewis, Cairney et al. 2011). In a study by Payne and colleagues it was shown that over daytime wakefulness both the features of objects and backgrounds of negative arousing scenes are being forgotten. Yet importantly, after a full night of sleep features of negative charged objects (but not backgrounds) are selectively preserved in memory (Payne, Stickgold et al. 2008). Latter effect could be interpreted in terms of the consolidation and preservation of important fragments of new experiences whiles irrelevant context information (such as the background) might be spared out. Also the authors reported in another study that sleep benefits consolidation of negatively charged stimuli over neutral ones (Payne and Kensinger 2011). Moreover, at least one study by Wagner and colleagues demonstrated that this consolidation is also relevant for long-term memory recall after years. In their study only emotionally arousing text material was better recalled after post-learning sleep as compared to periods of waking even when tested 4 years after learning (Wagner, Hallschmid et al. 2006). In this context it is also interesting to note that no difference was found between an early slow wave sleep (SWS) rich and a late rapid eye movement sleep (REM) rich sleep group with respect to the delayed memory recall. Yet, note that overnight emotional memory formation was more enhanced following REM-rich sleep (Wagner, Gais et al. 2001)

There is also evidence that in children (11-13yrs) emotional (declarative) memory benefits more from periods of sleep than wakefulness (Prehn-Kristensen, Göder et al. 2009) and furthermore that children might be using different sleep mechanisms in order to consolidate information. In children the great amount of SWS throughout early development seems to especially promote the consolidation of memories in the hippocampus-dependent declarative memory system (Backhaus, Hoeckesfeld et al. 2008; Wilhelm, Prehn-Kristensen et al. 2012). However, this slow-wave activity prevalence may counteract an immediate benefit from sleep for procedural memories, as typically observed in adults (e.g. Fischer, Wilhelm et al. 2007; for review see Wilhelm, Diekelmann et al. 2008; Prehn-Kristensen, Göder et al. 2009).

The mere presence of emotional stimuli during learning a procedural motor skill influences improvement of performance, in terms of accuracy and speed, both after sleep and after waking (Javadi, Walsh et al. 2011). Participants who learned this new skill with a negative image in the background demonstrated significantly greater enhancement of this skill across an offline retention interval than participant who trained with neutral or positive images in the background.

In general, a beneficial influence of sleep on emotional memory is evident. Yet it is to note that the picture is still ambiguous. While Walker and colleagues believe in a REM-dependent attenuation of emotional reactivity overnight, Baran and colleagues propose that the role of sleep for emotions is twofold. Besides the agreement that in general there is a beneficial effect of sleep for emotional memory the authors propose that sleep *protects* the emotional salience of a stimulus (Baran, Pace-Schott et al. 2012). Especially Baran and colleagues report that while emotional reactivity to negative pictures was greatly reduced over wake, the negative emotional response was relatively *preserved* over sleep and associated with greater time in REM.

In a next step we will consider the consequences of sleep deprivation on the formation and consolidation of newly acquired emotional material.

Sleep Deprivation

When participants are trying to form new memories following sleep deprivation, disturbances on encoding of especially positive and neutral stimuli is reported (Walker and Stickgold 2006). Moreover, Walker and colleagues indicated that there is a relative resistance of negative emotional memory even over sleep deprivation (for review see Saletin and Walker 2012). Interestingly a similar association had already been found earlier by Sterpenich and colleagues who reported no influence of sleep deprivation on recollection of negative arousing picture stimuli, but significant deterioration of positive and neutral stimuli following a lost night (Sterpenich, Albouy et al. 2007).

Altogether the results suggest that sleep deprivation profoundly destroys the ability to encode (especially not salient) material as well as to maintain freshly encoded (non-salient) memory traces. Whether negative stimuli are specifically less susceptible to forgetting or interference following sleep deprivation should be validated in future studies.

REM Sleep and Emotional Memory Consolidation

Without doubt, REMplays an important part in the consolidation of emotional memories (e.g. Greenberg, Pearlman et al. 1983; Wagner, Gais et al. 2001; Wagner and Born 2008; Nishida, Pearsall et al. 2009; Walker 2010; Payne 2011; Baran, Pace-Schott et al. 2012). When for example comparing 3 hours of REM-rich sleep versus early SWS-rich sleep or comparable times of waking, only the REM-rich condition facilitates the later recall of negative arousing narratives even if tested years thereafter (Wagner, Gais et al. 2001). Furthermore, after REM-rich sleep (relatively to SWS-rich sleep) subjects tend to rate emotional pictures seen before as more aversive (Wagner, Fischer et al. 2002). Latter finding stands in contrast to newer findings by Gujar and colleagues (Gujar, McDonald et al. 2011). Lately, it was demonstrated that emotional memory formation can also be manipulated pharmacologically. Wagner and colleagues (2005) tried to inhibit cortisol which usually is high in REM-rich sleep. The manipulation with metyrapone (a cortisol blocker) led to impaired consolidation of neutral but not emotional texts. Consequently, the authors speculated that the specific interaction between REM and the release of stress hormones like cortisol during post-learning sleep is adaptive and most critical for the consolidation of emotional memories (Wagner, Degirmenci et al. 2005). On the other hand Groch and colleagues blocked noradrenergic activity (primarily occurring during SWS and reported to be involved in linking the basolateral amygdala with the hippocampus) with clonidine and reported a disappearance of the retention advantage of emotional over neutral stories (Groch, Wilhelm et al. 2011). As clonidine is also known to have REM suppressive effects, it is difficult to assess whether an asscoiated mild REM suppression might have enhanced the pharmacologically induced attenuation of emotional memories.

Nishida and collegues also reported that more REMand shorter REM onset latency in a nap is positively correlated with the extent of emotional (picture) memory enhancement (Nishida, Pearsall et al. 2009). Interestingly in that nap paradigm improvement in emotional memory was directly related to an increase in (right) prefrontal EEG theta activity during REM (Nishida and Walker 2007; Nishida, Pearsall et al. 2009). It is to note that besides the characteristic theta oscillations (4-7 Hz), an increase of the level of acetylcholine (particularly in limbic systems and the forebrain (Walker 2010)), and an enhancement in cortisol concentrations (Born and Wagner 2004) is characteristic for REM. Cortisol is known to influence the hippocampus through glucocorticoid and mineralocorticoid receptors. Wagner and colleagues believe that an increase of cortisol in REM-rich late sleep might reduce the emotional impact of memories (Born and Wagner 2004) similar to a currently proposed model by Walker and colleagues (Walker 2009; Walker 2010).

Next we will shortly review related neuroimaging findings which demonstrate brain plasticity changes on a cortical and subcortical level.

Neuroimaging and Emotional Memory Consolidation

In general, it is known that learning of emotional stimuli is accompanied by strong activation of the amygdala and hippocampus (for review see Walker 2010). It has been shown that the amygdala accompanies and facilitates memory storage in emotionally charged memory tasks (e.g. Cahill, Haier et al. 1996; Cahill and McGaugh 1998; Hamann, Ely et al. 1999; Hamann 2001; Paré, Collins et al. 2002; Kilpatrick and Cahill 2003; Born and Wagner 2004; Wagner, Degirmenci et al. 2005; Sterpenich, Albouy et al. 2007). Sterpenich and colleagues for example revealed that after a full-night of sleep, recollection of emotional stimuli elicits stronger response in hippocampus and the medial prefrontal cortex, as compared to neural stimuli. Yet, 6 months thereafter the hippocampus is not activated anymore when that information is retrieved. This is taken as evidence for a (declarative) systems memory consolidation process where information is transferred from the hippocampus to more permanent cortical storage sites. Moreover, recollection of negative stimuli was associated with a hippocampo-neocortical response pattern in all subjects, but with a stronger response in an amygdalo-cortical network in sleep-deprived subject (Sterpenich, Albouy et al. 2007; Sterpenich, Albouy et al. 2009). The authors interpreted their findings as a possible subcortical “backup mechanism” which keeps track of emotional relevant (negative) material even in the case of sleep deprivation.

Payne and Kensinger reported correlations between successful retrieval of negatively charged stimuli and activation in the hippocampus, yet, regardless of the presence or absence of sleep (Payne and Kensinger 2011). To-date it appears unclear how long amygdala activation is needed for recollection of emotional stimuli and how strongly this dependence is modulated by post-learning sleep (for review see Sterpenich, Albouy et al. 2007). It is therefore highly relevant to consider and control the time between encoding and retrieval of the information as there are highly diverging findings concerning the speed of “systems consolidation”, or the transfer of initially hippocampus or amygdala driven responses to higher-cortical responses during retrieval.

As reviewed earlier, the amygdala has a strong modulating function in memory consolidation. When items are emotionally charged, the amygdala appears to facilitate hippocampal memory formation (e.g. Paré, Collins et al. 2002; Born and Wagner 2004; Wagner, Degirmenci et al. 2005). This widely held view builds upon the fact that the amygdala is involved in processing of emotions, whereas the hippocampus is known to be necessary for declarative and episodic memory formation. Since the participation of those two systems in the course of emotional memory consolidation is obvious, their reciprocal interaction is addressed in several neuroimaging studies. A recent study by Payne and

Kensinger using emotion-laden stimuli for example reported that after sleep the amygdala was more strongly connected to hippocampus and ventral medial prefrontal cortex as compared to a waking condition (Payne and Kensinger 2011). Importantly, connectivity changes were again specific to the retrieval of negative (but not neutral) study material.

It is known that in sleep-deprived subjects functional connectivity between amygdala and medial prefrontal cortex can be lost (see also Yoo, Gujar et al. 2007; Payne and Kensinger 2011). Yet, as seen in Sterpenich and colleagues (2007) there appears to be a kind of backup mechanism that prevents a complete deterioration of especially negatively charged emotional memories. In this case recollection might not depend upon hippocampo-neocortical networks but rather on alternative subcortical networks as also supported by Yoo and colleagues (2007). Specifically, the authors report greater connectivity between amygdala and the autonomic-activating centres in the locus coeruleus, as well as three times bigger extent of amygdala reactivity to aversive stimuli in the sleep deprived people (Yoo, Gujar et al. 2007). It can be speculated that after a sleep-deprived night a loss of mesial prefrontal mediated inhibition of the amygdala might lead to excessive emotional reactivityduring retrieval.

In summary it appears vital for us humans to memorize emotional material, specifically if of negative valence. Nature therefore seems to have come up with mechanisms to prevent forgetting of negatively charged information. With respect to brain plasticity changes, we generally agree with Diekelmann and colleagues (2009) who conclude and propose that "Patterns of emotional arousal that are induced during learning via amygdalar circuitry possibly become reactivated during REM sleep thereby strengthening memory traces and connectivity within hippocampo-neocortical networks."

The Influence of Stressful Emotions on Sleep

There is ongoing research concerning the influence of stress and emotions in general on sleep. In this context it is crucial to specify how exactly emotions or stressful events are elicited. Kim and Dimsdale (2007) distinguish three different types of stress, namely daily stressors, experimentally induced stress (like aversive films or simply a first night adaptation in the sleep laboratory) and real traumatic stress which is known to potentially even lead to severe psychiatric disorders such as posttraumatic stress disorder (PTSD) or major depression. In summary, very inconsistent results are evident in the literature, especially concerning the change of REM parameters following stress. Although Kim and Dimsdale (2007) could not reveal systematic differences between all of these different types of stressors in their systematic review (literature published between 1974 and 2004) they did find some consistent effects. Experimentally induced stress like first night adaptation or indwelling venous catheters resulted in less total sleep time (TST), less amount of SWS and REM , as well as longer sleep onset latencies together with a higher number of nightly awakenings. In contrast, experimental stress induced by aversive films appears to only cause marginal changes in (REM) sleep (Goodenough, Witkin et al. 1975; Levin, Strygin et al. 2002; Germain, Buysse et al. 2003). In people suffering from PTSD it seems that REM duration is decreased whereas REM latency is rather prolonged in most studies (Lavie, Hefez et al. 1979; Hefez, Metz et al. 1987). Interestingly, even sleep studies using experimentally induced stress - reviewed over the last 30 years – do not indicate consistent changes of sleep architecture.

Yet, it is to be noted that a recent study (Vandekerckhove, Weiss et al. 2011) does replicate early findings. The authors induced stress by provoking failure experience in different cognitive tasks (e.g. spatial abilities, counting or semantic tasks) using tasks which were impossible to solve (e.g., a related word had to be found for a group of three unrelated words). Participants were additionally told that they are doing cognitive tests which reflect their level of intelligence and their potential for future professional achievements. Moreover, the experimenter entered the experimental room during the tasks giving irritating comments and checking placement of electrodes. At the end of the task the experimenter explained, that the psychological measurements were erroneous and useless. After that kind of stress induction the authors found a significant increase in sleep fragmentation (higher amounts of number of awakenings and wake after sleep onset), decreased TSTand sleep efficiency, REM duration decrease as well as enhanced latency to SWS.

Overall it can be concluded that sleep tends to be more fragmented after stress exposure which is reflected in higher number of awakenings, decreased TST and decreased sleep efficiency. Concerning REM parameters, the results are highly contradictory with studies indicating REM increases (Goncharenko 1979; Cartwright and Wood 1991; Engdahl, Eberly et al. 2000) as well as decreases (Lavie, Hefez et al. 1979; Hefez, Metz et al. 1987; Aber, Block et al. 1989; Vitiello, Larsen et al. 1996; Prinz, Bailey et al. 2001; Scholle, Scholle et al. 2003) following emotional stress. Furthermore, shortened (Goncharenko 1979; Cartwright and Wood 1991) as well as prolonged (Kupfer, McPartland et al. 1974; Lavie, Hefez et al. 1979; Hefez, Metz et al. 1987) latency to the first REM episode during sleep has been reported.

For future research it seems important to not only specify the eliciting type of stress or emotions but to also focus on the individual coping strategy. Not only the subjective intensity but also the quality of the stressor might be a crucial determinant for subsequent sleep architecture changes. Last but not least, it needs to be assessed more systematically how perceived stress is altered over the course of a single, or even the course of several nights.

DO EMOTIONS CHANGE OVERNIGHT?

Emotional reactivity specifies the intensity of subjective or physiological activation to an emotional event. As this reactivation is often investigated in combination with questions about emotional memory, studies typically use pictures, word pairs or texts as stimulus material.

An actual model of affective brain processing (Walker 2009) suggests a close connection between emotional memory consolidation and the level of emotional reactivity (Walker and Van Der Helm 2009). In his “Sleep to remember and sleep to forget” – hypothesis (SRSF) Walker claims that people sleep to remember the facts of an emotional event, but at the same time to “forget” the affective tone of this event. More precisely, Walker states that emotional memory consolidation is strengthened (during REM), whereas the subjective and physiological emotional reactivity is reduced over sleep. Consequently, it should be possible to retrieve emotional experiences without the affective tone after successful sleep. The theory predicts that this decoupling takes place overnight, especially during REM, as this sleep stage provides the best biological state with increased activity in the limbic and paralimbic structures, marginal amount of aminergic (e.g. adrenalin, dopamine and serotonin) transmitter concentration as well as theta waves for integration of the emotional event into longterm-memory. It has to be tested if such a dissociation of emotion and related memory is reliably to identify and whether subjective traits may differentially mediate these overnight changes in emotional valence.

A study by Van der Helm et al. (2011) adds weight on earlier interpretations. The authors investigated negative and neutral pictures of the International Affective Pictures System (IAPS; Lang, Bradley and Cuthbert (2005)). Using functional Magnetic Resonance Imaging it was revealed that amygdala activity as well as subjective ratings of valence and arousal decreased over sleep, but were enhanced over the same amount of time when filled with daytime wakefulness. In addition, this described decrease in emotional reactivity overnight was significantly correlated with the extent of prefrontal gamma activity during REM. The authors took the association of reduced prefrontal gamma activity during REM with a stronger reduction in emotional reactivity overnight as evidence for the reduced central adrenergic activity mediating a depotentiation of the emotional tone overnight.

Further support for a specific role of REM in processing emotional events comes from another study of Walker'sgroup using midday naps and an emotional face recognition task. Naps, especially if they contained REM, reduced on the one hand the subjective ratings of face expressions of fear and anger and on the other hand increased perceived valence of happy expressions (Gujar, McDonald et al. 2011). Given that and earlier findings it is likely that REM therefore is not only involved in emotion depotentiation, but probably all stages of consolidation, from supporting the consolidation of salient emotional events, to various degrees of potentiation and depotentiation of emotional quality over night. Future studies should strive to disentangle the relation of REM with emotional reactivity changes overnight versus over daytime and also adopt more find-grained analysis of the distinct sleep patterns prevalent in REM (e.g., number of rapid-eye movements, gamma oscillations, theta oscillations, connectivity changes).

Another related study which investigated emotional memory performance simultaneously to emotional reactivity revealed partly diverging effects. Specifically, Baran and colleagues found a significant negative association of REM percentage (in the third quarter of the night) and emotional reactivity change overnight (Baran, Pace-Schott et al. 2012). Participants with more REM showed less decrease in subjective valence ratings from evening to morning (same pictures and intermingled new ones for recognition test), although all subjects did show less emotional reactivity ("arousal") after sleep. Interestingly, also an earlier study by Wagner and colleagues (2002) reported enhanced emotional reactivity (only on 'valence', but not 'arousal' scale) to negative pictures after REM-rich sleep in contrast to SWS-rich sleep or wakefulness. Enhanced emotional reactivity was also found after a full night of undisturbed sleep (comparable to REM-rich sleep only).

Altogether, it appears inconclusive in which way emotions are processed or altered over periods of sleep. Evidence indicates that REM is playing a key role, yet the exact nature of the relationship is unclear as REM has been found associated with decreased as well as increased emotional reactivity overnight. Further research is needed in order to clarify the exact role of REM in emotional processing and reactivity overnight. In light of the contradictory results it is suggested to consider further modulating factors such as individual differences on the level of personality traits or reappraisal skills and measure subjective emotional reactivity after stress induction over various time spans.

CONCLUSION

In summarizing, it can be concluded that emotional material, and specifically negatively charged information is more likely to be consolidated over periods of sleep. Negative emotions also stand out in the respect that even under conditions of sleep deprivation alternative "backup systems" may help to keep track of such potentially vital experiences.

The effects of various emotions on sleep architecture and sleep patterns is much less well understood. REM appears to play a key role in this respect, yet the exact association is to be identified.

Also data about the change of emotional reactivity overnight is ambiguous. However, evidence appears to accumulate that perceived emotional reactivity is generally decreasing over time.

Surprisingly there is much left to do, when it comes to sleep, memory and emotions. We hope scientists will be stimulated by this review and follow up on raised questions from various angles.

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