Research report

Sleep unbinds memories from their emotional context

Gaëtane Deliens*, Médhi Gilson, Rémy Schmitz and Philippe Peigneux*

UR2NF, Neuropsychology and Functional Neuroimaging Research Unit at CRCN — Centre de Recherches en Cognition et Neurosciences and UNI — ULB Neurosciences Institute, Université Libre de Bruxelles (ULB), Brussels, Belgium

A R T I C L E  I N F O

Article history:
Received 17 October 2012
Reviewed 16 November 2012
Revised 22 November 2012
Accepted 29 November 2012
Action editor Mike Kopelman
Published online xxx

Keywords:
Sleep deprivation
Memory consolidation
Emotion
Interference

A B S T R A C T

Consistent evidence nowadays indicates that sleep protects declarative memory from lexical interference. However, little is known about its effect against emotional interference. In a within-subject counterbalanced design, participants learned a list of word pairs after a mood induction procedure (MIP), then slept or stayed awake during the post-learning night. After two recovery nights, half of the list was recalled after a similar mood induction than at the encoding session (no interference condition) and the other half after a different mood induction (interference condition). Amongst participants for whom the MIP was effective, an emotional interference effect appeared only in the sleep-deprived condition, with a lower recall of word pairs subjected to contextual interference than of the other pairs. These findings support the hypothesis of a decoupling between memories and their “affective blanket” during post-learning sleep, protecting recent memories against emotional contextual interference.

© 2012 Elsevier Ltd. All rights reserved.

1. Introduction

After a learning episode, still fragile memory traces are gradually converted with time into more stable representations in long-term memory (McGaugh, 1966; Müller and Pilzecker, 1900). Growing evidence suggests that memory consolidation, or the process of trace stabilization and strengthening, preferentially occurs during sleep (Gais and Born, 2004; Maquet, 2001; Stickgold, 2005). Besides merely stabilizing memories however, sleep also contributes in protecting them against retroactive interference (Ellenbogen et al., 2009, 2006). In a classical AB–AC interference paradigm, Ellenbogen et al. (2006) asked participants to memorize a list of word pairs (AB), after which they spent a period of time either sleeping (at night) or awake (during daytime). At the second session and before retrieval of list AB, half of the participants memorized novel word pairs (AC), in which the first word of the pair was the same as in list AB, hence creating interference, whereas the other half directly proceeded to cued recall of list AB. In the non-interference condition, results showed a trend for a better recall of list AB after sleep than wakefulness. In the interference condition however, the beneficial effect of sleep...
was highly significant with a much better recall of list AB just after learning list AC, suggesting that memories consolidated during sleep are more resistant to retroactive interference. This effect was confirmed in a subsequent study in which participants were tested first in non-interference then in interference conditions within the same retrieval session (Ellenbogen et al., 2009). In the above studies, the material used to elicit interference was intrinsic to the learned material (word, engram), hence creating lexical interference. Still, it is not known whether extrinsic, contextual information would also induce interference effects. It is also not known whether sleep would prevent such interference to occur, especially in the domain of emotional interference, although there is a known effect of sleep on the consolidation of emotional memories.

It is now well established by various neuroimaging, neuropsychological and neural stimulation studies that memory is influenced by emotional arousal both at the memory encoding and memory consolidation stages (for review see Hamann, 2001), in such a way that emotional experiences are better remembered than neutral ones (e.g., Cahill, 2000; Dolcos et al., 2005; McGaugh, 2004; Phelps, 2004; Walker and Tarte, 1963). Most interestingly, it has been shown that a retention interval longer than 24 h leads to greater emotional arousal enhancement effects on declarative memory (Kleinsmith and Kaplan, 1963; LaBar and Phelps, 1998; Sharot and Yonelinas, 2007), suggesting a possible implication of sleep and/or time elapsed awake. Moreover, Hu et al. (2006) compared recall performance for negative and neutral pictures after a full night of sleep versus a same interval spent awake across the day. They found an emotional memory benefit after post-training sleep, validating the hypothesis of a sleep-dependent process in emotional memory consolidation. Furthermore, to avoid circadian confounds, Atienza and Cantero (2008) compared memory performance for emotional and neutral pictures after 1 week in participants deprived or not of sleep on the first post-learning night. Although, as expected, memory for both picture types was impaired in the sleep deprivation condition, performance was surprisingly better for emotional pictures suggesting that emotional stimuli are less sensitive to sleep deprivation; alternatively that the six recovery nights preferentially strengthened emotional altered memories. However, Wagner et al. (2001) demonstrated in a selective sleep deprivation paradigm that the second half of a night of sleep, richer in rapid eye movement (REM) sleep, is actually responsible for the beneficial effect of sleep on emotional texts as compared to neutral ones. In this study, participants studied brief texts having an emotional or a neutral content, and were then allowed to sleep during an interval of 3 h either covering the first part of the night of sleep (early sleep), richer in slow-wave sleep (SWS), or the second half (late sleep) dominated by REM sleep, or were kept awake during the same periods. Results disclosed a selective enhancement of memory for emotional texts following late, REM-rich sleep only (Wagner et al., 2001), persisting up to 4 years later (Wagner et al., 2006). REM sleep involvement was also confirmed in a nap paradigm (Nishida et al., 2009), in which enhancement in emotional memory after a 90-min nap was correlated with the amount of REM sleep. Finally, Payne et al. (2008) investigated whether sleep enhances memory for the emotional experience as a whole, or acts separately on different emotional memory constituents by enhancing only the affective component. Participants were presented pictures of neutral or negative objects on a neutral background and then had a recognition test on object and background separately after 12 h spent awake during daytime or 12 nighttime hours including sleep. Results showed that negative objects were consolidated at the expense of their background in the sleep-delayed condition, whereas both components were altered at similar rates in the wake-delayed condition, suggesting that sleep preferentially enhances the emotional components of memories.

All of these studies have investigated how sleep impacts on the consolidation of an emotional item or an emotional object in a neutral background. However, it remains unclear what would happen if the object is emotionally neutral but the background arouses emotions, or if the item to-be-learned is neutral but associated with a non-neutral mood at encoding. Kenealy (1997) showed that participants who learn and recall material in the same mood have better recall performance than participants who learn and recall in different moods, suggesting that a change of mood from learning to recall interferes with recall capacities (Bartlett and Santrock, 1979; Kenealy, 1997).

In this perspective, taking into account the proposal that sleep protects declarative memory (e.g., word pairs) against interference (Ellenbogen et al., 2009, 2006), we wondered whether this protective effect embraces the emotional component of novel memories, in particular when the emotional component is extrinsic to the learned material such as a different mood at the encoding and the recall sessions. To test this hypothesis, we designed a within-subjects study in which participants learned neutral word pairs after a mood induction procedure (MIP) (Mayer et al., 1995), then slept or were kept awake on the first post-training night, and were finally tested after two recovery nights either in the same or in a different mood than at the learning phase. To account for this effect known as mood-state dependent retrieval, Bower (1981) proposed the Network Theory of Affect. According to this theory, a network of nodes representing interconnected semantic concepts would constitute memory. Emotions would be units or nodes also integrated in this semantic network, and linked with propositions or assertions describing events during which the specific emotion was aroused. Hence when an emotional node is activated, emotion-related nodes in the semantic network would be activated also promoting their accessibility in mind. Consequently, when a similar emotional context takes place during the recall session, the same emotional nodes than at the encoding session are reactivated, eventually activating stimuli presented during the learning phase. In this case, the emotional context cues the learned material, hence a facilitation effect. On the other hand, when the emotional context at recall is different from the one experienced at the learning session, this facilitation effect cannot take place. Furthermore, a different emotional context may activate emotion-related concepts that will compete with the learned stimuli, hence creating interference.
2. Method

2.1. Participants

Twenty-six healthy participants gave written informed consent to participate in this study, which was approved by the local ethics committee. Due to irregular sleep pattern or floor effects in the memory task (recall score at delayed phase <10%), four participants were excluded from the statistical analyses. The 22 remaining participants (12 males, mean age ± SD 21.86 ± 2.38 years) met the following criteria: native French speakers, non-smokers, no history of neurological disorders or sleep disorders [Pittsburgh Sleep Quality Index (PSQI) total score <8, Buysse et al., 1989; Fatigue Severity Scale 2.68 ± 1.14, Krupp et al., 1989], no mood disorders (Beck’s Depression Scale <12, Beck et al., 1998), intermediate or neutral chronotype (Horne and Ostberg’s, 1976; Morningness–Eveningness Questionnaire: range 31–69), and verbal intelligence within normative values (Mill Hill Vocabulary Scale 26.24 ± 4, Deltour, 1993). They were required to keep regular sleep (RS) patterns during the week before and throughout the experiment, and to refrain from drinking alcohol or stimulant drinks (e.g., caffeine, energizers ...) before each testing session. To control for the regularity of sleep habits they were asked to wear an actimeter (DaqTix GbR, Oetzen, Germany) and to fill in daily sleep logs during the entire experiment. All participants participated both in the RS and sleep deprivation (SD); conditions were spaced 1 week apart, in a counterbalanced randomized order.

2.2. Material

2.2.1. Word pairs memory task

For the learning task, we created two parallel lists of 40 French unrelated words pairs [e.g., cheval – salon (horse – lounge)], composed of emotionally neutral bisyllabic nouns (Bonin et al., 2003; Messina et al., 1989; Syssau and Font, 2005), matched for lexical frequency (Content et al., 1990), imageability and concreteness (Desrochers and Bergeron, 2000), and randomly assigned across individuals to the sleep and sleep-deprivation (SD); conditions were spaced 1 week apart, in a counterbalanced randomized order.

2.2.2. MIP

The MIP was the translated French version of the original combined imagery vignettes and music procedure created by Mayer et al. (1995). Participants listened for 1 min to one of the following classic music pieces: Delibes’s Coppélia, Bach’s Brandenburg Concerto No.2 and Beethoven Symphony No.3 (happiness induction) and Chopin’s Préludes, Prokofiev’s Alexander Nevsky and Chopin’s Nocturne No.15 (sadness induction). Whilst listening, participants had to perform a guided imagery task on eight vignettes presented on the computer’s screen in a fixed order at 30-sec intervals. Each vignette was a descriptive sentence of a sad or a joyful situation (e.g., “A pet you were really fond of has died”). Participants were asked to imagine themselves emotionally engaged in each situation. The Affect Grid (Eich and Metcalfe, 1989) was administered before and after each MIP to assess changes in the emotional state attesting the effectiveness of the MIP. The Affect Grid is a nine lines by nine columns matrix in which the horizontal axis represents emotional valence and the vertical axis indicates arousal level, on a scale ranging from −4 (very sad/non-aroused) to +4 (very happy/aroused). The square in the center of the matrix represents neutral feelings. Participants were asked to tick the square that fitted best their current feelings.

2.2.3. Procedure

The study phase took place at day 1 in the evening (between 7 and 8 p.m.). First, participants were asked to fill in the Affect Grid (mood baseline). They were then administered the MIP (either sadness or happiness, counterbalanced). At the end of the induction procedure, they had to fill in again the mood questionnaire before learning the AB list. In this study phase, the 40 unrelated word pairs were displayed one by one on a computer screen for 3 sec each, followed by a white fixation cross for 3 sec that turned red after 2 sec to warn the participant of the transition to the next pair. Immediately after the learning session, there was an immediate cued recall procedure: the first word of each pair appeared on the computer screen and participants had to write the associated word. After the participant’s response, the computer provided the correct answer to help error-free consolidation of items. This cued recall procedure was repeated until participants were able to recall at least 30 word pairs (i.e., a 75% learning criteria). When a pair was correctly completed, it was not presented in subsequent trials to avoid over-consolidation through repetition. The presentation order of the word pairs changed after each presentation of the list to prevent serial learning. During the learning session and immediate recall phases the music piece used in the induction procedure was played in a continuous loop to help keeping participants in the induced mood. Finally, emotional state was assessed again using the Affect Grid.

Following the study phase, half of participants slept normally at home (RS) whereas the other half was sleep deprived (SD) for the whole night in controlled conditions (low luminance, quiet activities allowed, free water, hourly isocaloric snacks, no smoking, drinking alcohol or any stimulant drinks) under the experimenters’ supervision (Fig. 1). All participants then slept at home for two supplementary nights to ensure equivalent attentional levels in the RS and SD groups at the time of retesting.

At day 4, at the same time of day as at learning, participants were administered a cued recall procedure in which half of the pairs were recalled after a MIP congruent with the emotional context induced at the encoding session [non-interference context (NIC)], whereas the other half was recalled after an induction in a different mood [interference context (IC)]. More precisely, in the non-interference participants underwent the same MIP than at encoding unless the piece of music was different from the encoding session, but aimed at inducing the same mood. This procedure was aimed at precluding the hypothesis that any interference effect would be inherent to the musical piece per se. After having completed the MIP participants continued listening to the music piece, and provided the associated word upon presentation of the first word of the pair for 20 pairs from the learned...
list AB. In the interference emotional context, the MIP was aimed at inducing the opposite mood than at encoding, after which the 20 other word pairs were recalled in the same condition. The 20 words per interference condition were always the same in each condition at delayed recall but were randomly presented within each condition to avoid recency and primacy effects. The two phases were separated by a 20-min break to minimize interference of the first mood induction on the second one. During this break, participants had to fill in a questionnaire about their sleep habits (PSQI, Buysse et al., 1989) and were administered a psychomotor vigilance task (PVT, Dinges and Powell, 1985). Efficacy of the MIP was assessed using the Affect Grid before and after each MIP and after each recall session.

The following week, participants repeated the same procedure using a parallel version of list AB, while being engaged in the other post-training condition (i.e., RS or SD). Mood induction at learning was also opposite of the mood induced the preceding week (i.e., sadness vs happiness), in a counterbalanced manner.

To control alertness levels between experimental sessions, participants were administered the PVT and the Karolinska Sleepiness Scale (KSS) (Akerstedt and Gillberg, 1990) before each learning and test sessions. They also completed the PVT and KSS each hour during the sleep deprivation night. An overview of the experimental design is illustrated Fig. 1.

2.2.4. Statistical analyses
Statistical analyses were performed using Statistica 7.0 (Statsoft Inc., Tulsa, OK). Repeated and mixed measures analysis of variance tests (ANOVA) were conducted, followed by Tukey’s post-hoc tests. Significance was set at \( p \leq .05 \), two-tailed.

3. Results

3.1. Sleep and vigilance parameters
A repeated measures ANOVA on mean reported sleep duration during the experiment with factors Sleep (RS vs SD) and Session (Learning vs Recall) did not reveal any main effect of Sleep \( (F(1,21) = 3.17, p = .09) \) or Session \( (F(1,21) = 4.04, p = .06) \) nor interaction \( (F(1,21) = .01, p = .9) \) effects, indicating similar mean sleep duration before learning and recall sessions in each condition. During the first night after learning in the sleep condition, mean sleep duration was \( 8.03 \pm 1.41 \text{ h} \).

Repeated measures ANOVAs conducted on subjective (KSS scores) and objective (PVT mean reaction time) vigilance parameters with within factors Sleep (RS vs SD) and Session (Learning vs Recall) did not reveal any main effect of Sleep or Session or interaction (all \( p \)-values > .1 for KSS and PVT), indicating similar vigilance levels in all experimental conditions.

3.2. Efficacy of the MIP
A repeated measure ANOVA was computed on Affect Grid scores with within-subject factors Sessions (at encoding, congruent mood recall and incongruent mood recall) and Mood induced (happy vs sad) and disclosed no main effect of sessions \( (F(2,80) = 1.81, p > .17) \) but a main effect of mood \( (F(1,40) = 13.67, p < .001) \) and an interaction between sessions and mood \( (F(2,80) = 37.57, p < .001) \). Tukey post-hoc comparisons confirmed similar mood at encoding and retrieval in the congruent, non-interference mood condition both for happy \( (p > .9) \) and sad \( (p > .9) \) mood, and different moods in the incongruent, interference mood condition \( (all \text{ ps} < .001) \). However, inspection of individual Affect Grid scores also indicated that mood induction was not efficacious in all participants. Induction was considered efficacious when Affect Grid scores indicated mood evolution toward the desired mood (i.e., happiness or sadness). As 13 out of 22 participants only were in the same desired mood at encoding and retrieval in the non-interference condition, and in different desired moods in the interference condition, mood induction efficacy was introduced as a supplementary, between-groups factor in statistical analyses [efficacious \( (N = 13) \) vs non-efficacious \( (N = 9) \) mood induction] computed on recall performance for learned word pairs (see below).

3.3. Emotional interference on verbal memory consolidation
A mixed measure ANOVA was computed on the number of correctly recalled pairs with within-subject factors Sleep (RS vs SD) and Interference [recall in the same (IC) vs different...
In the efficacious mood induction group, Tukey’s post-hoc tests disclosed an interference effect in the SD condition with lower recall of word pairs subjected to mood interference than for the others (F1,20 = 4.36, p = .0499, ηp² = .18). All other effects were non-significant (p > .18).

In the efficacious mood induction group, Tukey’s post-hoc tests disclosed an interference effect in the SD condition with lower recall of word pairs subjected to mood interference than for the others (IC 6.31 ± 3.3 vs NIC 9.54 ± 4.39, p = .001), which was not present in the RS condition (IC 6.69 ± 4.03 vs NIC 7.38 ± 3.5, p = .94; see Fig. 2). Recall of word pairs not subjected to mood interference was higher in the SD condition than in the RS condition, both in the efficacious (p = .03) and non-efficacious (p = .03) mood induction groups. Recall of word pairs subjected to mood interference was higher in the SD condition than in the RS condition, with factors Sleep (RS vs SD) and Interference [recall in the same (IC) vs the different (NIC) emotional context] conducted on the 13 participants for whom mood induction was efficacious yielded similar results.

A repeated measures ANOVA on the number of correctly recalled pairs with within-subject factors Sleep (RS vs SD) and Interference [recall in the same (IC) vs different (NIC) emotional context] conducted on the 13 participants for whom mood induction was efficacious yielded similar results.

In the present study, we investigated how post-training sleep modulates the effect of contextual emotional interference on the delayed recall of verbal memories. First, our results replicate the finding that between-sessions congruency in the emotional context of neutral words enhances memory recall (Kenealy, 1997). Indeed, we found a group effect with higher recall when participants learned and recalled word pairs after the same MIP than when the MIP was different, suggesting a mood-state dependent retrieval. Furthermore, in participants for whom the MIP was effective, we found that post-training sleep actually reduces the mood-state dependent retrieval effect, whereas it was preserved in participants deprived of sleep on the first post-learning night. Indeed, we observed interference effects in the sleep deprivation condition due to higher recall of word pairs in the non-interference condition, rather than due to a lower recall performance in the interference condition. Hence, it suggests that sleep diminishes contextual emotional interference effect, thus reducing the facilitating effect of congruency between mood states at learning and retrieval.

As a whole, our results support the Sleep to Forget and Sleep to Remember (SFSR) proposal (van der Helm and Walker, 2009) that sleep facilitates the decoupling of declarative memories from their emotional context. According to this model, high concentrations of amnnergic neurotransmitters and amygdala activation during wakefulness facilitate the encoding of emotional memories in their affective context. During REM sleep however, whereas the rise of cholinergic activity and theta oscillations may participate in the reactivation of learned information eventually strengthening emotional memories (Jones and Wilson, 2005), the marked decrease in aminergic activity may in parallel lead to a depotentiation of the emotional tone initially associated with the learned element. It was therefore surmised that the specific neurochemical imbalance dominating REM sleep participates in the strengthening of recent memories while removing their learning-related affective blanket. As polysomnographic recordings were not obtained in the present study, we cannot here disambiguate the role of sleep stages, Interference (F1,12 = 6.89, p = .02) with higher recall in the non-interference than in the interference condition and a consistent Sleep by Interference effect (F1,12 = 10.56, p = .007). Tukey’s post-hoc tests revealed an interference effect in the SD condition with lower recall of word pairs subjected to mood interference than for the others (p < .001), which was not present in the RS condition (p = .63).

### 3.4. **Effect of mood type at learning**

Finally, we tested whether the mood type (happiness vs sadness) induced at learning had an impact on ulterior memory retrieval in the NIC. ANOVA for independent sample with factors Sleep (RS vs SD) and mood type (happiness vs sadness) failed to disclose mood-related differences in recall performance (F1,40 = .68, p = .41, ηp² = .017) nor Sleep by mood type interaction (F1,40 = .73, p = .40, ηp² = .018).
and especially of REM sleep, in this demodulation process, and can only attest to a sleep-related emotional unbinding effect on recall performance.

Looking at our results from the perspective of the SFSR model, it would be assumed that during post-learning sleep, after demodulation between the target learned items (i.e., the word pairs) and their affective tone (i.e., the emotional context created by the MIP), the latter would be removed according to the “sleep to forget” principle. For participants in the SD condition, sleep deprivation prevented the unbinding of the memory from its emotional context. Consequently in the SD group, putting participants at the delayed recall phase in the same mood as at learning would prime the retrieval of associated word pairs, whereas this process would be no longer effective for participants having slept after learning, and in whom the memory was dissociated from its emotional context. Accordingly, we have found that recall of word pairs is actually and paradoxically higher in the sleep deprived than in the sleep condition when the mood context is similar in the learning and recall sessions. Conversely, for sleep-deprived participants in whom mood induction was effective, inducing a different mood at retrieval would create an interference preventing access to the word pair still associated to its affective envelope. In the sleep condition, words unbound from their emotional context would become neutral and thus less sensitive to the effect of the emotional cuing in the non-interference condition. It should be noticed that this tentative explanation only applies for participants in whom mood induction was effective and well controlled, which makes difficult to interpret results obtained in participants for whom mood induction was not efficacious.

In participants for whom mood induction was not efficacious, we observed various patterns. Some participants were not in the same mood at encoding and retrieval in the non-interference condition and/or were not in the intended different moods in the interference condition; this is true for both the sleep and sleep-deprived conditions. Also, several participants were in a mood that was contrary to the expected mood induction. Why mood induction was not efficacious in all participants at any time of testing may be due to various reasons. First, it is known that personality factors such as trait emotional intelligence (Petrides and Furnham, 2003), impulsivity-thrill seeking, reward and punishment sensitivity (Zelenski and Larsen, 1999) may influence the efficacy of a laboratory MIP. Second, baseline mood may also exert an impact on subsequent mood induction efficacy. Indeed, if in a highly happy baseline mood before the sad MIP, the participant may have found it difficult to imagine himself emotionally engaged in the presented sad situations during the induction procedure, and vice-versa if departing from a quite sad baseline mood. Third, it is also possible that the MIP would have induced the expected mood but that the participant experienced difficulties in subjectively identifying this mood. Finally, one cannot exclude defensive mechanisms in participants reporting a mood opposite to what was expected. Further studies may use electrophysiological measures (skin conduction, pulse, cortisol levels ...) to compare self-rated mood questionnaires with physiological manifestations of the MIP. Studies should also investigate the potential relationships between individual variations in susceptibility to mood induction and processing of emotionally tagged memories during post-training sleep.

Coming back to the present study, it is difficult to determine the impact of a failure in the MIP on our results, since some participants in the non-efficacious mood induction group actually presented the expected mood in the sleep but not in the wake condition, and conversely. Consequently, this group is very heterogeneous, which makes analyses hazardous. Further studies conducted in a larger sample could allow distinguishing of participants who were not in the same mood at encoding and retrieval in the non-interference condition from those who were not in different desired moods in the interference condition; again in the sleep and sleep-deprived conditions separately. Hereafter, we will focus the discussion on findings in participants for whom mood induction was efficacious.

Our findings in this latter group are in line with neuroimaging findings. Indeed, it was shown using functional Magnetic Resonance Imaging (fMRI) that re-exposition to emotionally positive, negative or neutral pictures during a recognition session 72 h after learning results in post-training sleep-dependent changes in cerebral activation patterns (Sterpenich et al., 2007). Although sleep-deprived participants presented a poorer recollection of pictures than participants in the sleep post-learning condition, activity in the amygdala-cortical network during successful retrieval was reduced in the normal sleep condition only. This latter result can be explained considering that “sleep to forget” mechanisms were prevented from occurring in the sleep-deprived condition. Still, it should be noticed that this lack of reduction in learned item-associated emotional cerebral activity was observed only for negative but not positive or neutral pictures. In contrast, in the present study, recall performance did not differ as a function of the mood associated with word pairs (happiness or sadness), neither in the RS nor in the SD condition.

Although our findings suggest that sleep may help in dissociating recently learned memories from their emotional context, it remains to be clarified whether it applies specifically to the emotional tag of memories or in a general manner to their contextual background independently of its emotional quality. Indeed, it has been shown that manipulations of the background context between encoding and recall sessions also impact upon memory performance. Context-dependent memory has been related to multiple dimensions of the contextual background of learning including the physical environment (Godden and Baddeley, 1975; Smith, 1979, 1985), olfactory versus auditory modalities (Parker et al., 2007; Schab, 1990), room size, odors and background music (Parker et al., 2007). In this respect, a sleep-related reduction in the extent to which context affects retrieval was recently evidenced (CAINNEY et al., 2011). In this study, category-cued recall for a list of words took place 12 h after learning in the same room than at the encoding session, or in a second room different in size, odor and background music. Results showed better recall after sleep than wakefulness, but only when the environmental context was different between the encoding and recall sessions, again suggesting that post-learning sleep helps to decontextualize recently learned memory, eventually protecting it from the negative impact of contextual variations on retrieval. Contrary to SFSR model (van der Helm and Walker,
however, it was proposed that decontextualization essentially takes place during SWS. This proposal capitalized on the standard consolidation model (Marr, 1971; McClelland et al., 1995), by which novel information is initially encoded in the hippocampus then progressively transferred toward neocortical structures for long-term storage. SWS is thought to participate in the process of memory consolidation by strengthening cortico–cortical connections while weakening hippocampo–cortical connections, thus allowing memories to become independent of the hippocampus while integrating in neocortical networks (Diekelmann and Born, 2010). As contextual information is hippocampus-dependent (Davachi et al., 2003; Davachi and Wagner, 2002) and hippocampus presents limited storage capacity, Cairney et al. (2011) proposed that contextual components are removed during SWS with weakening of the hippocampo–cortical connections. Further dedicated studies should investigate whether memory decontextualization preferentially takes place during SWS (Cairney et al., 2011) or REM sleep (van der Helm and Walker, 2009) in relation with the emotional nature of the contextual components associated with the learning episode.

Finally, it may be noticed that a control condition is absent from our study. Although such a control condition would provide further information, we decided not to include it in this experiment for methodological reasons. Indeed, in our study subjects heard sad or happy music during the word pairs presentation and recall phases, in order to help keeping them in the induced mood. As it can be considered more difficult to study and recall words pairs with background sounds, subjects in the control condition should also have been proposed background music, i.e., a neutral music piece. However, it is extremely difficult to ensure that music is emotionally neutral (Krumhansl, 1997), and consequently we decided not to include this control condition to avoid this methodological bias.

5. Conclusion

In summary, we show here that sleep reduces the facilitating effect of emotional congruency between learning and retrieval contextual background, suggesting that post-training sleep releases recently learned memories from their emotional context. Thanks to the sleep–dependent decoupling of memory from its affective tag and the removing of the latter, the emotional reactivity associated with these items is reduced, consequently making memories less sensitive to emotional cueing.

Acknowledgment

The authors thank Isaline Caudron for help in data acquisition, and two anonymous Reviewers for their insightful and constructive comments on a prior version of this manuscript. GD, MG and RS are Research Fellows at the Belgian Fonds National de la Recherche Scientifique (FNRS). This study has been conducted with support of FNRSCC grant 1.5.184.10.F and FRSM grant 3.4.594.08.F.

References


