RESEARCH ARTICLE

# Offline consolidation of procedural skill learning is enhanced by negative emotional content

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**Abstract**   It is now well established that both procedural skills and episodic memories consolidate across periods of offline retention, and most particularly across periods of sleep. Such consolidation has been demonstrated to be more marked for emotional than for neutral episodes, but the interaction between emotionality and the offline consolidation of procedural skills has yet to be investigated. Here, we address this issue by examining the impact of an emotional background context at encoding upon the subsequent consolidation of mirror tracing, a well-studied procedural skill. We also consider the importance of sleep for such consolidation by manipulating the retention interval (over a day, overnight, or over 24 h containing normal sleep). Our data show significantly greater offline improvements in the accuracy of mirror tracing when negative emotional content is present during the training phase when compared to when neutral or positive content is present. Furthermore, consolidation across a night of sleep is associated with faster and more accurate performance than consolidation across a day of wakefulness. These novel findings show that the emotional context in which a procedural skill is learned can impact upon subsequent offline consolidation.

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## Introduction

One of the most potent factors known to modulate memory is emotion, and numerous studies have demonstrated that experiences that elicit emotion at the time of learning lead to superior subsequent recollection (Cahill 2000; McGaugh and Roozendaal 2002; Cahill and Alkire 2003; McGaugh 2004; Phelps 2004). Furthermore, these effects of emotion on memory appear to increase as the delay between learning and testing increases (Kleinsmith and Kaplan 1963; Walker and Tarte 1963; Levonian 1972). This has led to the suggestion that emotional content may not only facilitate the initial encoding of information, but may also enhance the subsequent "offline" consolidation of memory processing, and it is even more pronounced if offline consolidation contains a period of sleep (Wagner et al. 2001; Payne et al. 2008; Walker 2009). To date, the investigation of how emotional content impacts upon consolidation has focused principally on declarative memory (Brown and Kulik 1977; Plihal and Born 1997; Ochsner 2000; Wagner et al. 2001; Kensinger et al. 2006; Payne et al. 2008). Interestingly, within declarative memory, the emotional content of stimuli such as texts (Wagner et al. 2001) or scenes (Payne et al. 2008; Nishida et al. 2009) has been shown to interact with sleep-dependent consolidation such that emotional items are more strongly consolidated across sleep than neutral items (for review see (Walker 2009). While these studies have deepened our understanding of the effects of emotion on consolidation of episodic memories, the possible modulatory role that emotions may have on procedural learning and offline

consolidation remains unknown. Here, we investigate how emotion modulates the consolidation of a procedural skill governed by memory systems known to be distinct from those involved in the types of declarative memory that is more commonly associated with emotional influences.

Mirror tracing is a procedural learning task in which subjects trace a figure with a stylus while viewing their hand, the stylus and the figure reflected in a mirror. The participants' task is to trace a curve (usually the border of a figure). The observed horizontal hand movement is left intact, whereas the vertical hand movement is mirrored. With practice, subjects trace the figure more quickly and make fewer errors (departures from the figure). Such sensorimotor skill tasks are used to study motor learning in patients with declarative memory problems due to amnesia (Milner 1962), Alzheimer's Disease (Gabrieli et al. 1993), Huntington's disease (Gabrieli et al. 1997) or patients with cerebellar dysfunction (Sanes et al. 1990). The mirror-tracing task has also been used to study learning and the effects of distributed practice (Snoddy 1920; Adams 1987). Furthermore, it has been used in studies showing consolidation across sleep in both patients and healthy participants (Plihal et al. 1999; Rouleau et al. 2002; Gais and Born 2004; Göder et al. 2004; Marshall et al. 2004; Nissen et al. 2006; Schabus et al. 2006; Fogel et al. 2007; Göder et al. 2007; Hornung et al. 2007, 2008; Tamaki et al. 2008; Kloepfer et al. 2009; Prehn-Kristensen et al. 2009; Nissen et al. 2010; Seeck-Hirschner et al. 2010). Previous studies have shown offline consolidation of procedural memory without any emotion manipulation (Walker et al. 2002; Robertson et al. 2004; Press et al. 2005; Robertson and Cohen 2006; Cohen and Robertson 2007; Nishida and Walker 2007) during wakeful retention intervals as well as an interval including sleep (Plihal and Born 1997; Maquet et al. 2000; Stickgold et al. 2000; Fischer et al. 2002; Laureys et al. 2002; Walker and Stickgold 2004).

In this report, our primary aim was to examine the effect of emotion on offline consolidation of the mirror-tracing task. We embedded the training portion of this task in negative, positive and neutral contexts in order to examine the impact of such emotional content upon subsequent offline consolidation. Participants were assigned to 'emotion' groups such that equal numbers were trained in each emotional context.

As a secondary aim of the study, we wished to test for an interaction between the modulatory effect of training in a specific emotional context and the influence of sleep during the retention interval. We therefore examined the contribution of sleep to the offline consolidation of a learnt skill and searched for interactions between such sleep-related consolidation and the emotional valence presented during training. Our design included three experimental groups: one which obtained no sleep in between the training and testing sessions (day group), and two which obtained nocturnal sleep (night and 24-h groups) between the training and testing sessions. The 24-h group was included as a control for the possibility that performance differences between the day and night groups might be associated with diurnal variations in performance instead of differences between consolidation obtained across wake and sleep.

## Materials and methods

### Participants

Ninety-nine participants (mean age 25.63, SD 3.08) took part in the study in 9 groups, comprised of the combination of retention type (day/night/24 h) and emotional content conditions (negative/positive/neutral). Table 1 shows the number of participants in each group. Sixteen further participants (8 women, mean age 22.53, SD 2.04) were recruited to rate the stimulus images for valence and arousal (rating from 1 to 9). Informed consent was obtained from all participants. All participants had normal or corrected-to-normal vision, and all were screened to exclude those with a history of neurological trauma, psychiatric disorder, sleep disturbance or irregular sleep patterns. They agreed to be drug, alcohol and caffeine free for 24 h prior to and during the study period. All subjects were right-handed. No participant was taking any centrally acting medications. The local institutional ethics committee approved general procedures.

### Stimuli

Stimuli consisted of faces which were negative, positive or neutral in content. To ensure that these differed

**Table 1** Number of participants in each group; Participants were assigned to one of 9 different groups according to retention type (day/night/24 h) and the emotional content of the experiment (negative/positive/neutral)

| Emotion | Negative | | | Positive | | | Neutral | | |
|---|---|---|---|---|---|---|---|---|---|
| Retention type | Male | Female | Total | Male | Female | Total | Male | Female | Total |
| Day | 5 | 7 | 12 | 5 | 7 | 12 | 6 | 6 | 12 |
| Night | 6 | 6 | 12 | 6 | 6 | 12 | 6 | 6 | 12 |
| 24 h | 5 | 4 | 9 | 4 | 5 | 9 | 5 | 4 | 9 |

significantly in valence, but not in arousal, 34 participants (healthy participants, aged 18–26, 18 women) rated the images for valence and arousal using the scales developed by Bradley and Lang (1994). Independent sample $t$-tests revealed a significant difference between the valence scores of positive and negative images ($t(338) = 18.43$, $P < 0.001$) but no significant difference in the arousal score ($t(338) = 0.922$, $P = 0.35$).

Figure 2 shows the stimuli. The border of each stimulus was specified by an 8-pixel wide green contour, $\sim 0.25°$ of visual angle. The start point for tracing was specified by a red dot on the top of each stimulus boarder. To ensure that stimuli from all three valences were associated with the same set of boundary contours for tracing, the boundary of the negative images was also imposed upon positive and neutral stimuli. In total, 5 different tracing templates were used. The first of these was just used for rehearsal in the first phase of the first session and in the first trial of the second session. Tracing performance for the first template was not considered in the overall performance of the participant in either of the sessions.

Apparatus

The mirror-tracing task was performed using a PC. Stimuli were presented on a 17″ colour monitor with 75 Hz refresh rate, subtending approximately $8 \times 13°$ of visual angle. Stimuli were presented on a black background and 53 cm from participants' eyes. Participants used a regular mouse to trace the border. The sampling frequency of mouse position was 100 Hz. The movement of the pointer on the screen was in the opposite direction of the movement of the hand of the participant in both horizontal and vertical directions, rather than just the vertical direction as in mirror-tracing tasks that use a mirror and mechanical apparatus.

Eye tracking was used to trace eye movements of participants in the day and night groups during both the first and second sessions. Eyes of participants in the 24-h group were not tracked. The eyes of 8 of the 72 participants were not tracked due to incompatibility of their glasses to the eye-tracker. Two criteria were considered: number of fixation points per second and number of saccades off the border and into the content of the stimuli.

Experiment procedure

The experiment was composed of two sessions (training and testing) with either a 12- or 24-h retention interval in between these. The timeline and design is shown in Fig. 1a. Participants were asked to leave the laboratory after the first session and to follow their normal daily routine while abstaining from daytime naps. Night and 24-h groups were

asked to obtain at least 6 h of nocturnal sleep. Activity during the retention interval and before the first session was monitored using log books in which sleep/wake times, foods and drinks consumed, and the quality of the dreams were recorded.

At the beginning of each session, participants completed the Stanford Sleepiness Scale (SSS) (Hoddes et al. 1973), a standard measure of subjective alertness, and performed a simple finger-tapping task to evaluate their alertness (Zimmermann and Fimm 1995).

The finger-tapping task was composed of two different configurations, Fig. 1b, c. In the first configuration, participants were asked to press a key corresponding to the visual cues (shown as filled circle) using both index fingers (left index finger for left circle and right index finger for right circle), Fig. 1b. In the second configuration, they were asked to use their right hand index, middle and ring fingers to respond to spatial location of each cue, respectively, from left to right, Fig. 1c. In both configurations, the cue remained steady until a response was logged, and this was followed by a screen including two (for the first configuration) or three (for the second configuration) blank circles presented for 100 ms. Participants were instructed to respond as fast and as accurately as possible in all conditions. The task continued for 70 repetitions of which the first 10 were discarded. Two participants who performed with less than 90% accuracy on the remaining 60 repetitions were withdrawn from the experiment (both due to low accuracy on the second session, one in the day group and one in the night group). These participants are not included in Table 1. The mean (correct) response time was used as performance measure.

In the mirror-tracing task, participants were asked to use the mouse with their right hand to move the pointer on the green border of the stimuli, tracing it clockwise as quickly and as accurately as possible. Movement of the pointer on the screen was mirrored in both horizontal and vertical directions. Both tracing time and performance accuracy were used for data analysis. Performance accuracy was calculated as:

$$\text{Performance (\%)} = 100 \times (\text{number of pixels traced on the green border/total number of traced pixels})$$

Tracing time was the total time taken to trace a stimulus, from start to finish.

Tracing began from the red dot on top of the stimuli and feedback on performance accuracy was shown after each tracing trial.

The first session of mirror tracing comprised two phases (Fig. 1). In Phase A, participants traced the stimulus #1 (Fig. 2) repeatedly until the performance passed 80% accuracy. In Phase B, participants traced stimuli #s 2–5
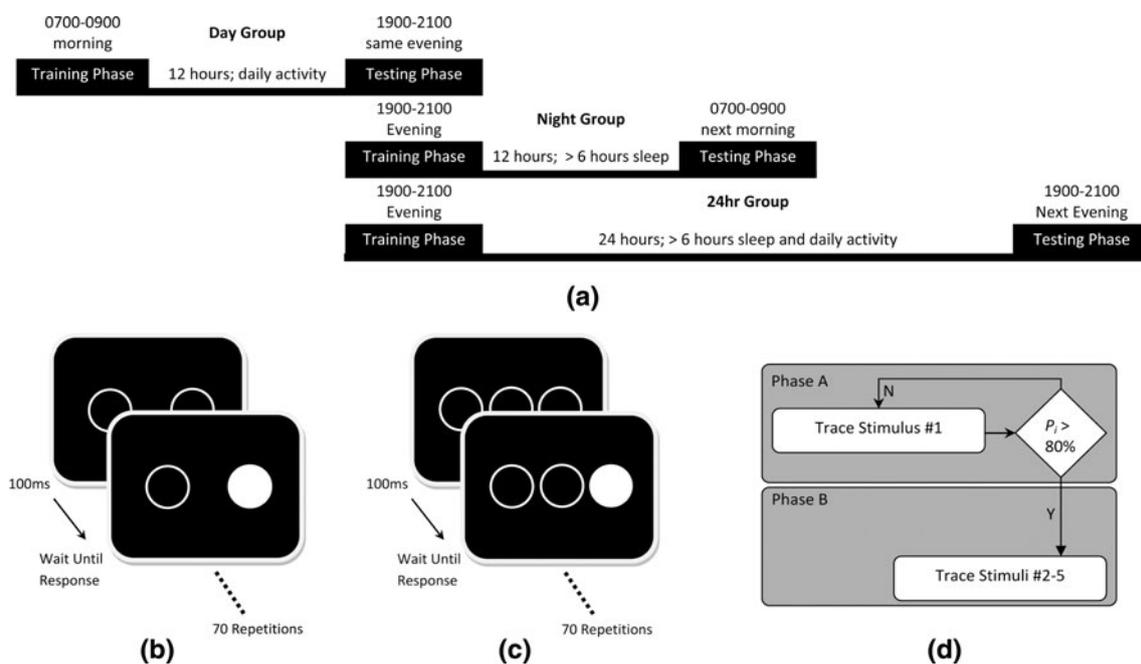
**Fig. 1** (**a**) The timing of the three groups; Participants were assigned to one of three different groups (day, night and 24 h). The retention interval was 12 h for the day and night groups and 24 h for the 24-h group. Participants could attend the test anytime between 7–9 a.m. and 7–9 p.m. for the morning and evening sessions, respectively.

(**b**) Shows the first configuration in which participants were asked to press a key corresponding to each of the *circles* using both index fingers. (**c**) In this task, participants were asked to use their right hand index, middle and ring fingers. (**d**) Procedure of the first session

once each. Performance and tracing time were averaged across all four Phase B trials.

In the second session, participants traced the five emotionally neutral stimuli in a fixed order as shown in Fig. 2. Performance and tracing time were averaged across all five tracing trials in the second session. Importantly, because all participants traced the same stimuli in the testing session, this assessment was comparable for those who had encoded with each of the three emotional types.

Performance improvement, calculated as mean change in performance accuracy from the first to second session, was used to compare the performance change from the first session to the second session between the groups.

## Results

### Performance accuracy

The main goal of the study was to investigate the effects of emotion at encoding on consolidation of a procedural task as a function of time. Performance improvement is shown in Fig. 3a for each experimental group. A $3 \times 3$ ANOVA with retention type (day/night/24 h) and emotional background at encoding (negative/positive/neutral) as between subject factors for performance accuracy improvement (final performance value for the second session minus final

performance value for the first session) indicated an effect of retention type ($F(2, 90) = 5.21$, $P < 0.01$), and an effect of emotional content ($F(2, 90) = 4.85$, $P < 0.01$), but no interaction ($F(4, 90) = 0.38$, $P > 0.2$). Planned comparison $t$-tests revealed greater improvements ($P < 0.01$) in those who were trained with stimuli in a negative context than in those who were trained in either positive or neutral contexts, Fig. 3b. Post hoc $t$-tests also showed significant improvements ($P < 0.01$) in night and 24-h groups compared to the day group, Fig. 3c.

Because participants traced the border of the novel stimuli just once in phase B of the first session and once more in the second session, the higher ability of the negative emotional group shows that they learnt the mirror-tracing skill rather than simply memorising the shape of the boarders which were traced in the first session. Improvements therefore relate to their skill in performing the task, rather than in retracing a learned pattern.

### Tracing time

In addition to accuracy of performance, tracing time was also altered after the offline retention interval. To study the impact of the three emotional backgrounds and of retention type upon this change (2nd session minus 1st session), we conducted a $3 \times 3$ ANOVA with retention type (day/night/ 24 h) and emotional background at encoding (negative/
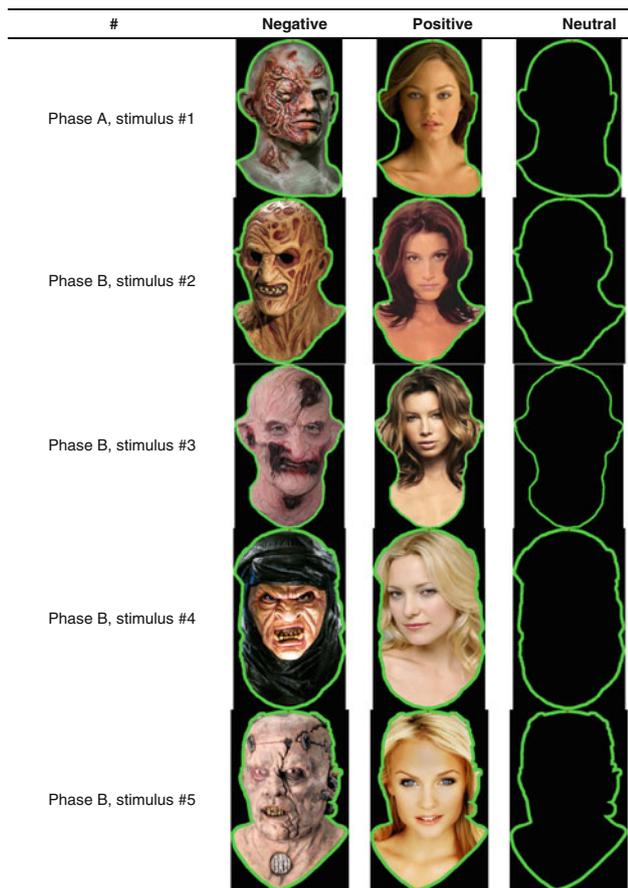
**Fig. 2** Different stimuli in three sets of emotional contents; images of horror masks, female faces and blank content were used for negative, positive and neutral emotional contents, respectively. The border of the horror masks (the *green* outline) was used as the tracing template in all the three sets of emotional contents

positive/neutral) as factors. This revealed a significant effect of retention type ($F(2, 90) = 3.85$, $P < 0.05$), with tracing time markedly impaired after consolidation across 12 h of wake, but not across 12 or 24 h including sleep, Fig. 4a. There was no effect of emotional content, and no interaction between retention type and emotion. Post hoc *t*-tests showed that tracing time was significantly more impaired across retention in the day group than in the night and 24-h groups ($P < 0.05$), Fig. 4c. Furthermore, planned comparison *t*-tests performed to investigate the a priori hypothesis that training in an emotional context would lead to greater consolidation revealed a significant difference between the tracing time of the participants in the negative emotional group and positive and neutral emotional groups ($P < 0.05$), Fig. 4b.

Finally, examination of the relationship between performance improvement and tracing time impairment revealed a significant correlation (day group $r = -0.56$, $P < 0.05$, night group $r = -0.75$, $P < 0.01$, 24-h group $r = -0.64$, $P < 0.05$), showing that accuracy and speed

changed together, e.g. the less accuracy improved the more speed decreased.

## Gender

To ensure that the gender of background images did not interact with participant gender, we compared the performance of male and female participants on all three types of stimulus background. A $2 \times 3$ ANOVA with participant gender (female/male) and stimulus emotionality (negative/ positive/neutral) as between subject factors for performance improvement revealed no main effect of gender and no interaction of gender and emotion ($P > 0.50$ for the comparisons). As there were no effects of gender, data from male and female participants were combined in all other analyses. While some studies have reported effects of gender on memory for emotional information (Bremner et al. 2001; Burton et al. 2004; Cahill et al. 2004) (for review see (Hamann and Canli 2004)), others have not. It may be that gender-related traits, rather than gender per se, influence memory (Cahill et al. 2004) or that only particular paradigms elicit robust effects of gender on emotional memory.

## Alertness

To examine the alertness of the participants at the beginning of each session, we conducted a multivariate $3 \times 3 \times 2$ ANOVA with retention type (day/night/24 h), emotion (negative/positive/neutral) and session number (first and second sessions) as between subject factors and with the Stanford Sleepiness Scale (SSS) rating and mean response time for correctly responded trials for the two configurations of finger-tapping task as independent factors. This revealed no significant effects in any of the comparisons ($P > 0.50$), showing that neither sleepiness nor alertness differed across groups or sessions.

## Initial performance and learning

The procedure of the first session required participants to repeat the rehearsal using a single stimulus until their performance passed a certain criterion (80% accuracy). To compare the participants' baselines on the learnt skill, we examined final performance at the end of the first session, learning rate (measured as number of repetitions of the first phase of training needed to reach the 80% criteria) and tracing time (as the mean value of the tracing time of the last 4 tracing trials in each session) using a multivariate $3 \times 3$ ANOVA with retention type (day/night/24 h) and emotion (negative/positive/neutral) as between subject factors. None of these analyses revealed a significant result (see Table 2), showing that the experimental groups were
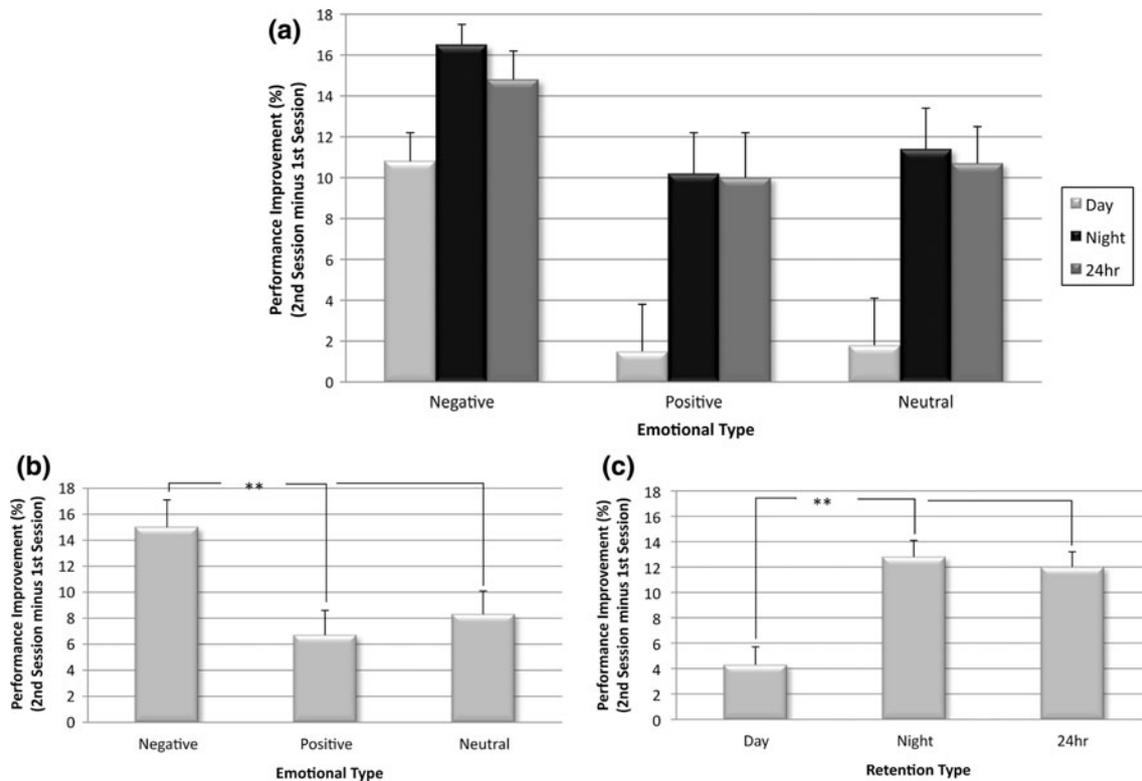
**Fig. 3** Performance changes across an offline delay. (**a**) Performance improvement from the first session to the second session, comparison between different emotional contents and different retention types. (**b**) Comparison between groups experiencing different background emotions with different retention types collapsed. (**c**) Comparison between different retention types with different emotions collapsed. **P < 0.01, *Error bars* = SD
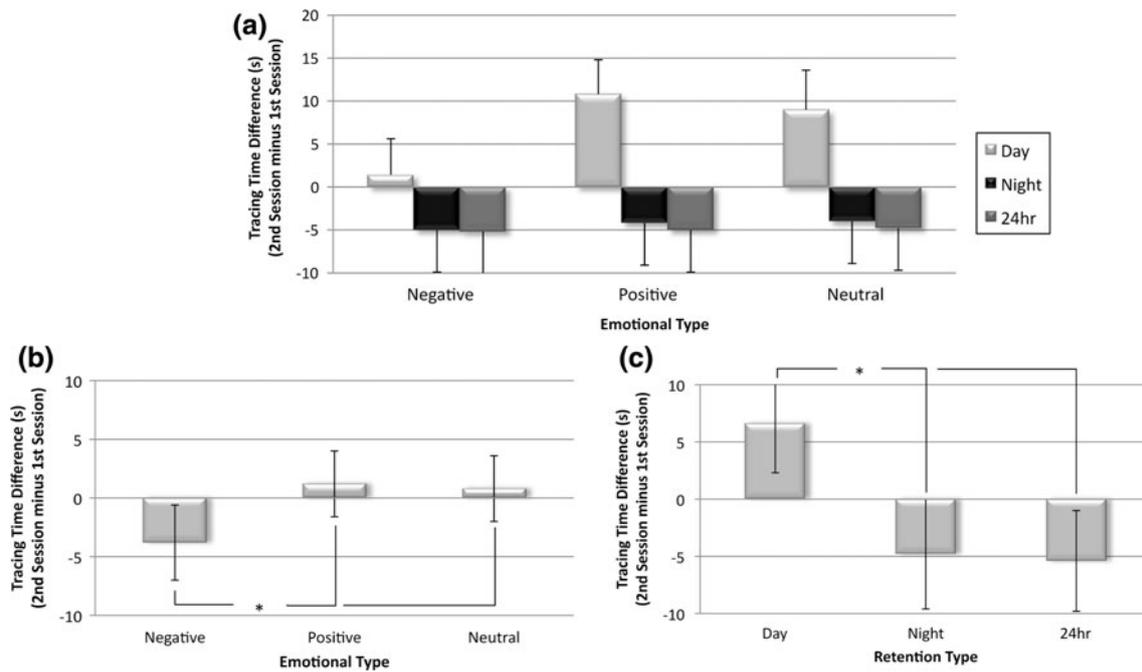


**Fig. 4** Changes of tracing time across an offline delay. (**a**) Changes in tracing time from the first to the second session. (**b**) Tracing time difference for groups with different retention type. (**c**) Tracing time difference for different emotional content for the day group. The positive values show longer tracing time, indicating reduction of tracing speed for the 1st session compared to the 2nd session. *P < 0.05, *Error bars* = SD

**Table 2** Summary of mean value of performance accuracy (%) and tracing time (s) of participants in different groups at the end of the first session

| Configuration | Emotional type | | | | | |
| --- | --- | --- | --- | --- | --- | --- |
| | Performance accuracy (%) | | | Tracing time (s) | | |
| Retention type | Negative | Positive | Neutral | Negative | Positive | Neutral |
| Day | 81.9 (4.8) | 80.2 (5.0) | 78.7 (5.8) | 48.6 (8.1) | 50.2 (6.8) | 48.2 (6.9) |
| Night | 79.4 (5.1) | 78.5 (5.3) | 81.4 (4.7) | 45.9 (7.5) | 47.8 (7.2) | 49.7 (6.6) |
| 24 h | 78.8 (5.0) | 81.1 (4.8) | 80.3 (5.1) | 49.1 (7.5) | 48.4 (8.2) | 52.3 (7.1) |

The numbers in the parentheses show the standard deviation

balanced for learning ability, or the level of skill obtained during training, $3 \times 3$ ANOVA with retention type and emotional content as independent variables ($P > 0.50$ in all the comparisons). Finally, examination of the relationship between learning rate and subsequent improvement between the first and second sessions revealed no significant correlation ($P > 0.50$).

### Eye-tracking data

Eye tracking was used throughout the experiment, in both session one and two, for day and night groups. We conducted a multivariate $2 \times 2 \times 3$ ANOVA with session number (first/second), retention type (day/night) and emotional type (negative/positive/neutral) as between subject factors with mean number of fixation points per second and mean number of saccades off the border and into the content of the stimuli for the last 4 tracing trials as independent variables. This ANOVA indicated no significant effects in any of the conditions ($P > 0.70$ for all the comparisons). This result showed that participants were not distracted with the internal content of the stimuli and their gazing point was kept on the border throughout the tracing trials.

### Data from log sheets

Participants in the night and 24-h groups reported two nocturnal sleeps, one the night before the first session and one in between the two sessions. Participants in the day group reported one nocturnal sleep before the first session. To ensure that these sleep episodes were of comparable duration prior to each session, we conducted a $5 \times 3$ ANOVA with retention type—day group (night before the first session)/night group (night before the first session)/night group (night in between the two sessions)/24-h group (night before the first session)/24-h group (night in between the two sessions—and emotion (negative/positive/neutral) as between subject factors for duration of nocturnal sleep acquired from sleep and activity-log diaries.

This analysis showed no significant effect in any of the comparisons ($P > 0.50$ in all the comparisons). None of the participants reported nocturnal sleep of less than 6 h, and none reported unpleasant dreams. Participants in day and 24-h groups did not nap during the day in between their two sessions.

Overall, these measures show that participants in all the groups were well matched for alertness.

## Discussion

In contrast to the diversity of studies on the contribution of emotion to explicit memory, studies on interaction of emotion and implicit memory have mostly focused on conditioning (Adolphs et al. 1995; Adolphs 2008; Maren 2008; Sah et al. 2008; Ehrlich et al. 2009). The main goal of the current investigation was to examine the impact of different emotional contexts during encoding upon the subsequent offline consolidation of procedural learning. To investigate this, we imbedded three different types of emotional stimuli, negative, positive and neutral, as background images during the encoding phase of a mirror-tracing task. Our data extend the literature by showing that the presence of negative content at encoding enhances subsequent performance (after a 12- or 24-h delay) on this procedural task in terms of both speed and accuracy. 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 participants who trained with neutral or positive images in the background. Our findings are discussed below.

### Emotional valence at encoding influences procedural learning

Interactions between the limbic and motor systems have been studied extensively (Haegelen et al. 2009) but, to our knowledge, the impact of such interactions upon the offline

consolidation of a procedural task have not been examined. Here, we show that the presence of negative stimuli at encoding boosts the subsequent offline enhancement of procedural memory. In contrast to studies of skill learning in a neutral context which did not report improvement of the learnt skill with simple passage of time (e.g. without sleep) (Plihal and Born 1997; Walker et al. 2002; Robertson et al. 2004; Press et al. 2005; Robertson and Cohen 2006; Cohen and Robertson 2007; Nishida and Walker 2007), we show that the presence of negative emotional content at encoding is associated with subsequent offline consolidation across both sleep and wake and leads to improved performance, Fig. 3(a).

Our observation of superior postconsolidation performance by subjects exposed to negative stimuli during training suggests that the presence of negatively arousing emotions at encoding may contribute to the offline consolidation of this procedural task. In addition to its role in encoding fear, converging findings from animal and human studies provide compelling evidence that the amygdala, which responds strongly to negatively arousing emotions (for review see (LeDoux 2000; Adolphs 2008; Seymour and Dolan 2008; Ehrlich et al. 2009; Roozendaal et al. 2009)), is critically involved in the acquisition and retention of lasting memories of emotional experiences (for review see (McGaugh 2004; LaBar and Cabeza 2006)). The amygdala is ideally situated to mediate interactions between negative emotion experienced during the learning of a procedural task and during offline consolidation of that task because it has both cortical and subcortical connections to the Basal Ganglia, a key player in the motor system which is also known to be critical for procedural memory (Kandel et al. 2000; Gazzaniga 2004). Connections between primary motor cortex, the limbic lobe and the basolateral complex of the amygdala (Morecraft and Van Hoesen 1998) and topographic projections from these regions to primary and supplementary motor cortices (Morecraft and van Hoesen 1992) provide a possible anatomical basis for interactions between emotional responses and motor learning. Other pathways which may contribute to such modulatory effects involve subcortical areas (Haber et al. 1995; Chikama et al. 1997; Ferry et al. 2000) and also interactions between limbic regions and basal ganglia through 'basal ganglia loops' (Heimer et al. 1982; Groenewegen and Berendse 1994; Haber 2003).

Interestingly, although we found a strong impact of negative context upon subsequent consolidation, our data showed no parallel influence of positive context. This null finding differs from studies of declarative memory which have shown facilitated memory for positive material (Maddock 1999; Cahill 2000; McGaugh and Roozendaal 2002; Cahill and Alkire 2003; McGaugh 2004; Phelps 2004; Richardson et al. 2004). Because we used nonstandard positive stimuli, which were only rated as mildly emotional (mean arousal score 3.82 for negative stimuli and 4.05 for positive stimuli rating between 1 and 9) this result could mean that our stimuli did not have a strong enough positive valence to elicit an effect. Alternately, it is possible that positive emotional valence does not interact with offline consolidation of procedural memory in the same manner as negative emotional valence. Further investigation necessary to study the effect of positively arousing stimuli in the consolidation of procedural memory with standard valenced images, e.g. Eckman faces.

The role of sleep

In keeping with prior examinations of how sleep impacts on procedural skill learning (Plihal et al. 1999; Rouleau et al. 2002; Gais and Born 2004; Göder et al. 2004; Marshall et al. 2004; Nissen et al. 2006; Schabus et al. 2006; Fogel et al. 2007; Göder et al. 2007; Hornung et al. 2007, 2008; Tamaki et al. 2008; Kloepfer et al. 2009; Prehn-Kristensen et al. 2009; Nissen et al. 2010; Seeck-Hirschner et al. 2010), we showed that participants who obtained at least 6 h of nocturnal sleep (night and 24-h groups), performed mirror tracing faster and more accurately than participants who did not sleep (the day group). Interestingly, this enhancement was more apparent for both speed and accuracy in the negative emotional content group (post hoc $t$-test $P < 0.05$, see Figs. 3 and 4), suggesting that encoding in a negative context may lead to greater consolidation during subsequent sleep. This finding is reminiscent of work on declarative memory which has shown that sleep selectively enhances memory for emotionally arousing episodes (Kleinsmith and Kaplan 1963; Walker and Tarte 1963; Levonian 1972; Plihal and Born 1997; LaBar and Phelps 1998; Walker et al. 2002; Sharot and Phelps 2004; Nishida and Walker 2007). Because arousal was balanced between our positive and negative stimuli, the observed effect is most parsimoniously linked to the negative valence of these stimuli and is therefore in line with a prior suggestion (Sterpenich et al. 2007) that negative information is preserved across retention periods when neutral and positive information is lost, even if this preferential retention requires the recruitment of additional neural systems.

Circadian influences on performance

The 24-h group were included to control for the possibility that differences in the time of day of at which training and testing sessions occurred might explain differences between performance of the day (trained in the morning and tested in the evening) and night (trained in the evening

and tested in the morning) groups due to the impact of tiredness, fluctuations in attention, or other circadian factors. Because the second session of the 24-h group and the second session of the day group were both conducted at the same time of the day (e.g. in the evening), comparison of results from these two sessions can be used to test for the impact of sleep during retention in a manner which is independent of time of the day. The fact that performance of the 24-h group was comparable to performance of the night group in terms of accuracy and speed, both of which were significantly higher than in the day group, helps to discount any concern about circadian influence on performance. In combination with the nonsignificant difference between Sleep and Wake groups in the SSS ratings, finger-tapping speed and accuracy, number of training tracing trials, and performance base-line in the first session, these data suggest that the night of sleep obtained after the training session by both night and 24-h groups was associated with superior subsequent performance of the learnt skill. Our data additionally suggest that sleep stabilised memory for the learnt skill and protected it from slowing down during wakefulness since the 24-h group, who experienced 12 h of wakeful retention after their nocturnal sleep, showed no slowing in tracing speed (Fig. 4).

Limitations of the study

One limitation in this study relates to the stimuli. Because the faces we used were not controlled for sex, facial expression, complexity or the contrast between the image and the green 'border'. It is possible that these factors may have contributed to our results (Gujar et al. 2010; van der Helm et al. 2010). Nevertheless, the observed modulatory effect of emotion on offline consolidation of procedural memory of mirror tracing is an overall contribution of different types of emotional contents regardless of variation within an emotional group. Considering the result of the control experiment in which participants rated the stimuli on scales of arousal and valence, we conclude that negative valence is an influential factor on the observed effect.

## References

Adams JA (1987) Historical review and appraisal of research on the learning, retention, and transfer of human motor skills. Psychol Bull 101:41–74

Adolphs R (2008) Fear, faces, and the human amygdala. Curr Opin Neurobiol 18:166–172

Adolphs R, Tranel D, Damasio H, Damasio A (1995) Fear and the human amygdala. J Neurosci 15:5879–5891

Bradley M, Lang P (1994) Measuring emotion: the self-assessment manikin and the semantic differential. J Behav Ther Exp Psychiatry 25:49–59

Bremner J, Soufer R, McCarthy G, Delaney R, Staib L, Duncan J, Charney D (2001) Gender differences in cognitive and neural correlates of remembrance of emotional words. Psychopharmacol Bull 35:55

Brown R, Kulik J (1977) Flashbulb memories. Cognition 5:73–99

Burton L, Rabin L, Vardy S, Frohlich J, Wyatt G, Dimitri D, Constante S, Guterman E (2004) Gender differences in implicit and explicit memory for affective passages. Brain Cogn 54:218–224

Cahill L (2000) Neurobiological mechanisms of emotionally influenced, long-term memory. Prog Brain Res 126:29

Cahill L, Alkire M (2003) Epinephrine enhancement of human memory consolidation: interaction with arousal at encoding. Neurobiol Learn Mem 79:194–198

Cahill L, Gorski L, Belcher A, Huynh Q (2004) The influence of sex versus sex-related traits on long-term memory for gist and detail from an emotional story. Conscious Cogn 13:391–400

Chikama M, McFarland N, Amaral D, Haber S (1997) Insular cortical projections to functional regions of the striatum correlate with cortical cytoarchitectonic organization in the primate. J Neurosci 17:9686–9705

Cohen D, Robertson E (2007) Motor sequence consolidation: constrained by critical time windows or competing components. Exp Brain Res 177:440–446

Ehrlich I, Humeau Y, Grenier F, Ciocchi S, Herry C, Lüthi A (2009) Amygdala inhibitory circuits and the control of fear memory. Neuron 62:757–771

Ferry A, Ongur D, An X, Price J (2000) Prefrontal cortical projections to the striatum in macaque monkeys: evidence for an organization related to prefrontal networks. J Comp Neurol 425:447–470

Fischer S, Hallschmid M, Elsner AL, Born J (2002) Sleep forms memory for finger skills. Proc Natl Acad Sci 99:11987–11991

Fogel S, Smith C, Cote K (2007) Dissociable learning-dependent changes in REM and non-REM sleep in declarative and procedural memory systems. Behav Brain Res 180:48–61

Gabrieli JDE, Corkin S, Mickel SF, Growdon JH (1993) Intact acquisition and long-term retention of mirror-tracing skill in Alzheimer's disease and in global amnesia. Behav Neurosci 107:899

Gabrieli JDE, Stebbins GT, Singh J, Willingham DB, Goetz CG (1997) Intact mirror-tracing and impaired rotary-pursuit skill learning in patients with Huntington's disease: evidence for dissociable memory systems in skill learning. Neuropsychology 11:272–281

Gais S, Born J (2004) Low acetylcholine during slow-wave sleep is critical for declarative memory consolidation. Proc Natl Acad Sci USA 101:2140–2144

Gazzaniga M (2004) The cognitive neurosciences. Bradford Books, Cambridge, MA

Göder R, Boigs M, Braun S, Friege L, Fritzer G, Aldenhoff J, Hinze-Selch D (2004) Impairment of visuospatial memory is associated with decreased slow wave sleep in schizophrenia. J Psychiatr Res 38:591–599

Göder R, Scharffetter F, Aldenhoff J, Fritzer G (2007) Visual declarative memory is associated with non-rapid eye movement sleep and sleep cycles in patients with chronic non-restorative sleep. Sleep Med 8:503–508

Groenewegen H, Berendse H (1994) Anatomical relationships between the prefrontal cortex and the basal ganglia in the rat. In: Thierry A-M (ed) Motor and cognitive functions of the prefrontal cortex. Springer, Berlin, pp 51–77

Gujar N, McDonald S, Nishida M, Walker M (2010) A role for REM sleep in recalibrating the sensitivity of the human brain to specific emotions. Cereb Cortex. doi:10.1093/cercor/bhq064

Haber S (2003) Integrating cognition and motivation into the basal ganglia pathways of action. In: Bedard MA, Agid Y, Chouinard S, Fahn S, Korczyn AD, Lesperance P (eds) Mental and behavioral dysfunction in movement disorders. Humana Press, New Jersey, pp 35–50

Haber S, Kunishio K, Mizobuchi M, Lynd-Balta E (1995) The orbital and medial prefrontal circuit through the primate basal ganglia. J Neurosci 15:4851–4867

Haegelen C, Rouaud T, Darnault P, Morandi X (2009) The subthalamic nucleus is a key-structure of limbic basal ganglia functions. Med Hypotheses 72:421–426

Hamann S, Canli T (2004) Individual differences in emotion processing. Curr Opin Neurobiol 14:233–238

Heimer L, Switzer R, Hoesen G (1982) Ventral striatum and ventral pallidum: components of the motor system. Trends Neurosci 5:83087

Hoddes E, Zarcone V, Smythe H, Phillips R, Dement WC (1973) Quantification of sleepiness: a new approach. Psychophysiology 10:431–436

Hornung O, Regen F, Danker-Hopfe H, Schredl M, Heuser I (2007) The relationship between REM sleep and memory consolidation in old age and effects of cholinergic medication. Biol Psychiatry 61:750–757

Hornung O, Regen F, Warnstedt C, Anghelescu I, Danker-Hopfe H, Heuser I, Lammers C (2008) Declarative and procedural memory consolidation during sleep in patients with borderline personality disorder. J Psychiatr Res 42:653–658

Kandel ER, Schwartz JH, Jessell TM (2000) Principles of neural science. McGraw-Hill, Health Professions Division, New York

Kensinger E, Garoff-Eaton R, Schacter D (2006) Memory for specific visual details can be enhanced by negative arousing content. J Mem Lang 54:99–112

Kleinsmith L, Kaplan S (1963) Paired-associate learning as a function of arousal and interpolated interval. J Exp Psychol 65:190–193

Kloepfer C, Riemann D, Nofzinger E, Feige B, Unterrainer J, O'Hara R, Sorichter S, Nissen C (2009) Memory before and after sleep in patients with moderate obstructive sleep apnea. J Clin Sleep Med 5:540

LaBar K, Cabeza R (2006) Cognitive neuroscience of emotional memory. Nat Rev Neurosci 7:54–64

LaBar K, Phelps E (1998) Arousal-mediated memory consolidation: role of the medial temporal lobe in humans. Psychol Sci 9:490–493

Laureys S, Peigneux P, Perrin F, Maquet P (2002) Sleep and motor skill learning. Neuron 35:5–7

LeDoux J (2000) Emotion circuits in the brain. Annu Rev Neurosci 23:155–184

Levonian E (1972) Retention over time in relation to arousal during learning: an explanation of discrepant results. Acta Psychol 36:290–321

Maddock R (1999) The retrosplenial cortex and emotion: new insights from functional neuroimaging of the human brain. Trends Neurosci 22:310–316

Maquet P, Laureys S, Peigneux P, Fuchs S, Petiau C, Phillips C, Aerts J, Del Fiore G, Degueldre C, Meulemans T, Luxen A, Franck G, Van Der Linden M, Smith C, Cleeremans A (2000) Experience-dependent changes in cerebral activation during human REM sleep. Nat Neurosci 3:831–836

Maren S (2008) Pavlovian fear conditioning as a behavioral assay for hippocampus and amygdala function: cautions and caveats. Eur J Neurosci 28:1661

Marshall L, Molle M, Hallschmid M, Born J (2004) Transcranial direct current stimulation during sleep improves declarative memory. J Neurosci 24:9985–9992

McGaugh J (2004) The amygdala modulates the consolidation of memories of emotionally arousing experiences. Annu Rev Neurosci 27:1–28

McGaugh J, Roozendaal B (2002) Role of adrenal stress hormones in forming lasting memories in the brain. Curr Opin Neurobiol 12:205–210

Milner B (1962) Les troubles de la memoire accompagnant des lesions hippocampiques bilaterales. In: Passant P (ed) Centre de la Recherche Scientifique. Physiologie de l'hippocampe. Paris, pp 257–272

Morecraft R, van Hoesen G (1992) Cingulate input to the primary and supplementary motor cortices in the rhesus monkey: evidence for somatotopy in areas 24c and 23c. J Comp Neurol 322(4):471–489

Morecraft R, Van Hoesen G (1998) Convergence of limbic input to the cingulate motor cortex in the rhesus monkey. Brain Res Bull 45:209–232

Nishida M, Walker M (2007) Daytime naps, motor memory consolidation and regionally specific sleep spindles. PloS One 2:e341

Nishida M, Pearsall J, Buckner R, Walker M (2009) REM sleep, prefrontal theta, and the consolidation of human emotional memory. Cereb Cortex 19:1158

Nissen C, Kloepfer C, Nofzinger E, Feige B, Voderholzer U, Riemann D (2006) Impaired sleep-related memory consolidation in primary insomnia—a pilot study. Sleep 29:1068–1073

Nissen C, Kloepfer C, Feige B, Piosczyk H, Spiegelhalder K, Voderholzer U, Riemann D (2010) Sleep-related memory consolidation in primary insomnia. J Sleep Res. doi:10.1111/j.1365-2869.2010.00872.x

Ochsner K (2000) Are affective events richly recollected or simply familiar? The experience and process of recognizing feelings past. J Exp Psychol Gen 129:242–261

Payne JD, Stickgold R, Swanberg K, Kensinger EA (2008) Sleep preferentially enhances memory for emotional components of scenes. Psychol Sci 19(8):781–788

Phelps E (2004) Human emotion and memory: interactions of the amygdala and hippocampal complex. Curr Opin Neurobiol 14:198–202

Plihal W, Born J (1997) Effects of early and late nocturnal sleep on declarative and procedural memory. J Cogn Neurosci 9:534–547

Plihal W, Pietrowsky R, Born J (1999) Dexamethasone blocks sleep induced improvement of declarative memory. Psychoneuroendocrinology 24:313–331

Prehn-Kristensen A, Göder R, Chirobeja S, Breßmann I, Ferstl R, Baving L (2009) Sleep in children enhances preferentially emotional declarative but not procedural memories. J Exp Child Psychol 104:132–139

Press D, Casement M, Pascual-Leone A, Robertson E (2005) The time course of off-line motor sequence learning. Cogn Brain Res 25:375–378

Richardson M, Strange B, Dolan R (2004) Encoding of emotional memories depends on amygdala and hippocampus and their interactions. Nat Neurosci 7:278–285

Robertson E, Cohen D (2006) Understanding consolidation through the architecture of memories. Neuroscientist 12:261

Robertson E, Pascual-Leone A, Miall R (2004) Current concepts in procedural consolidation. Nat Rev Neurosci 5:576–582

Roozendaal B, McEwen B, Chattarji S (2009) Stress, memory and the amygdala. Nat Rev Neurosci 10:423–433

Rouleau I, Decary A, Chicoine A, Montplaisir J (2002) Procedural skill learning in obstructive sleep apnea syndrome. Sleep 25:401–411

Sah P, Westbrook R, Luthi A (2008) Fear conditioning and long-term potentiation in the amygdala what really is the connection? Ann N Y Acad Sci 1129:88

Sanes JN, Dimitrov B, Hallett M (1990) Motor learning in patients with cerebellar dysfunction. Brain 113:103

Schabus M, Hödlmoser K, Gruber G, Sauter C, Anderer P, Klösch G, Parapatics S, Saletu B, Klimesch W, Zeitlhofer J (2006) Sleep spindle-related activity in the human EEG and its relation to general cognitive and learning abilities. Eur J Neurosci 23:1738–1746

Seeck-Hirschner M, Baier P, Sever S, Buschbacher A, Aldenhoff J, Göder R (2010) Effects of daytime naps on procedural and declarative memory in patients with schizophrenia. J Psychiatr Res 44:42–47

Seymour B, Dolan R (2008) Emotion, decision making, and the amygdala. Neuron 58:662–671

Sharot T, Phelps E (2004) How arousal modulates memory: disentangling the effects of attention and retention. Cogn Affect Behav Neurosci 4:294–306

Snoddy GS (1920) An experimental analysis of a case of trial and error learning in the human subject. Psychol Rev 124:1–78

Sterpenich V, Albouy G, Boly M, Vandewalle G, Darsaud A, Balteau E, Dang-Vu TT, Desseilles M, D'Argembeau A, Gais S, Rauchs G, Schabus M, Degueldre C, Luxen A, Collette F, Maquet P (2007) Sleep-related hippocampo-cortical interplay during emotional memory recollection. PLoS Biol 5:e282

Stickgold R, James LT, Hobson JA (2000) Visual discrimination learning requires sleep after training. Nat Neurosci 3:1237–1238

Tamaki M, Matsuoka T, Nittono H, Hori T (2008) Fast sleep spindle (13–15 Hz) activity correlates with sleep-dependent improvement in visuomotor performance. Sleep 31:204

van der Helm E, Gujar N, Walker M (2010) Sleep deprivation impairs the accurate recognition of human emotions. Sleep 33:335–342

Wagner U, Gais S, Born J (2001) Emotional memory formation is enhanced across sleep intervals with high amounts of rapid eye movement sleep. Learn Mem 8:112–119

Walker M (2009) The Role of Sleep in Cognition and Emotion. Ann N Y Acad Sci 1156:168–197

Walker M, Stickgold R (2004) Sleep-dependent learning and memory consolidation. Neuron 44:121–133

Walker E, Tarte R (1963) Memory storage as a function of arousal and time with homogeneous and heterogeneous lists. J Verbal Learn Verbal Behav 2:113–119

Walker M, Brakefield T, Morgan A, Hobson J, Stickgold R (2002) Practice with sleep makes perfect sleep-dependent motor skill learning. Neuron 35:205–211

Zimmermann P, Fimm B (1995) Test for attentional performance (TAP). PsyTest, Herzogenrath, Germany