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.

Keywords Consolidation · Procedural memory · Procedural learning · Emotion · Sleep

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 Tart 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; Pihal 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>
<thead>
<tr>
<th>Emotion</th>
<th>Negative</th>
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<th>Positive</th>
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<th>Neutral</th>
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<tr>
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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, $\sim 0.25^\circ$ 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 $8 \times 13^\circ$ 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:

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

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.
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 borders 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/positive/neutral) as between subject factors for tracing time improvement (final tracing time for the second session minus final tracing time for the first session).
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
balanced for learning ability, or the level of skill obtained
during training, 3 × 3 ANOVA with retention type and
emotion 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 signifi-
cant 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 con-
ducted a multivariate 2 × 2 × 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 signifi-
cant 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 × 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 noc-
turnal 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 back-
ground 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. Par-
ticipants who learned this new skill with a negative image
in the background demonstrated significantly greater
enhancement of this skill across an offline retention inter-
val 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

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

<table>
<thead>
<tr>
<th>Configuration</th>
<th>Emotional type</th>
<th>Performance accuracy (%)</th>
<th>Tracing time (s)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Negative</td>
<td>Positive</td>
<td>Neutral</td>
</tr>
<tr>
<td>Day</td>
<td>81.9 (4.8)</td>
<td>80.2 (5.0)</td>
<td>78.7 (5.8)</td>
</tr>
<tr>
<td>Night</td>
<td>79.4 (5.1)</td>
<td>78.5 (5.3)</td>
<td>81.4 (4.7)</td>
</tr>
<tr>
<td>24 h</td>
<td>78.8 (5.0)</td>
<td>81.1 (4.8)</td>
<td>80.3 (5.1)</td>
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</table>

The numbers in the parentheses show the standard deviation.
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 providing feedback), 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 (Ledaou 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 1992) 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. Alternatively, 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; Goëder 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.

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