

Offline processing of memories induced by perceptual visual learning during subsequent wakefulness and sleep: A behavioral study

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To further characterize perceptual memory consolidation during sleep, we used a coarse orientation discrimination task in which participants had to discriminate the orientation of orthogonal gratings occluded by increasing levels of noise. In a first study ($N = 11$), we showed that the learning effect in this task is retinotopic (position-specific) and orientation specific. In a second experiment, we assessed the effect of nocturnal sleep, as opposed to the effect of time, on perceptual learning. A first group of participants was trained in the morning, tested in the evening and retested the next morning (morning–evening–morning, MEM, $N = 11$); a second group was trained in the evening, tested the next morning, and retested in the evening (evening–morning–evening; EME; $N = 12$). Between training and testing, EME subjects improved significantly more (after a night of sleep) than MEM subjects (after 12 waking hours). Similarly, between test and retest, performance of MEM subjects (after a full night of sleep) improved significantly more than in EME subjects (after 12 further waking hours). These results suggest a beneficial effect of sleep on coarse orientation discrimination. Further studies are needed to characterize the neural correlates of this perceptual learning and the offline consolidation of perceptual memory.

Keywords: perceptual learning, memory, orientation discrimination, sleep, circadian rhythms, behavior

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Introduction

Visual perceptual learning depends primarily on practice. Daily training repeated over days or weeks is typically associated with monotonic improvement of visual skills (Crist, Li, & Gilbert, 2001; Karni & Sagi, 1991; McKee & Westheimer, 1978; Tsodyks & Gilbert, 2004; Vogels & Orban, 1985), which can eventually be retained for months or years (Karni & Sagi, 1993; Schoups, Vogels, & Orban, 1995). However, another finding is that perceptual learning significantly improves *between* training sessions (Karni et al., 1995), suggesting that perceptual memory is processed offline, in the absence of any practice.

Sleep is thought to facilitate these offline processes which consolidate visual perceptual learning. This contention is based on several experiments using the texture discrimination task (TDT; Gais, Plihal, Wagner, & Born, 2000; Karni, 1995; Karni & Sagi, 1991). In this task, a target screen is briefly displayed, followed by a blank

screen for a variable stimulus onset asynchrony (SOA), which is followed by a mask. The target screen consists of three diagonal bars in one quadrant of the screen, in either a vertical or a horizontal array, displayed against a background of horizontal bars. Central fixation is enforced by a letter discrimination task at the center of the screen. Performance is quantified by the minimum SOA required to reach 80% accuracy on the target discrimination task.

Total sleep deprivation during the night which follows the initial training to the TDT annihilates the gain in performance otherwise observed 2 days later if sleep is allowed during this particular night (Stickgold, James, & Hobson, 2000). This visual skill learning is particularly sensitive to selective deprivation of rapid eye movement (REM) sleep (Karni, Tanne, Rubenstein, Askenasy, & Sagi, 1994) but might in fact require the ordered succession of non-REM and REM sleep phases to be optimally consolidated (Mednick, Nakayama, & Stickgold, 2003; Stickgold, Rittenhouse, & Hobson, 1999). Importantly, these effects are not likely to be explained by a circadian factor since a daytime nap is as good as a night

of sleep for texture discrimination learning (Mednick, Arman, & Boynton, 2005; Mednick et al., 2002, 2003).

Learning to discriminate visual texture in the TDT is assumed to be associated with local neural changes taking place in early visual areas which code for visual field positions where targets were presented and for the eye which has been trained (Karni & Sagi, 1991; Lu, Chu, Doshier, & Lee, 2005; Schoups & Orban, 1996; Schwartz, Maquet, & Frith, 2002). For this reason, it is considered as an important model of memory consolidation because some local neural processes under consideration in this task might be relevant for our understanding of sleep-related consolidation (Maquet, 2001) in more complex, distributed, memory systems such as declarative, or procedural (Albouy et al., 2006; Gais et al., 2007; Orban et al., 2006; Peigneux et al., 2006; Schabus et al., 2004; Sterpenich et al., 2007).

Unfortunately, the specific mechanisms underlying this speeded texture discrimination are still uncertain. In the TDT, visual skill learning could equally be related to the improved detection of the target orientation by enhanced connections between orientation-selective cells or enhanced responses of neurons that respond to the target, or to a reduced background noise through improved lateral inhibitory connections, allowing an easier target discrimination (Karni & Sagi, 1991). In addition, although the results mentioned above provide compelling evidence for a beneficial effect of sleep on speeded visual texture discrimination, they do not guarantee that these effects can be generalized to any visual perceptual learning task.

Our aim was to study the effect of sleep on perceptual learning using a different visual task that is based on the coarse discrimination of a basic visual feature. The task should allow the reliable characterization of perceptual skill learning in humans at both behavioral and macroscopic systems levels. In addition, perceptual learning induced by the task should show between-session gains in performance, suggesting offline memory processing, especially across time periods filled with sleep.

We employed a coarse orientation discrimination task during which participants have to discriminate between two orthogonal orientations of a grating, displayed peripherally and embedded in noise. These oriented stimuli are known to activate striate and extrastriate neurons (Desimone, Schein, Moran, & Ungerleider, 1985; Hubel & Wiesel, 1968; Merigan & Maunsell, 1993; Schiller, Finlay, & Volman, 1976; Vogels & Orban, 1990). This coarse orientation discrimination should be contrasted with fine orientation discrimination (Vogels & Orban, 1985). In the fine task, subjects need to discriminate just noticeable differences (JND) in orientation while in the present coarse task the difficulty of the task is manipulated by the degree of partial occlusion of the grating by the noise while not affecting the large orientation difference. The latter manipulation is expected to affect the strength of the response in visual cortical areas to the oriented grating: The smaller the occluding

noise, the stronger the evoked response measured with electrodes in extrastriate area V4 (Franko, Seitz, & Vogels, 2006) and presumably also in V1. Nishina, Seitz, Kawato, and Watanabe (2007) employed a similar discrimination task and showed perceptual learning using such stimuli in the context of a rapid serial presentation of central letter stimuli. We adapted their task to study the effect of sleep on coarse orientation discrimination. In this paper, we show in a first experiment that the visual skills acquired after repeated training over a week in this adapted coarse orientation discrimination task are specific to the trained orientations and visual field quadrant. In a second experiment, we describe the time course of visual perceptual learning in this task over 24 hours and provide evidence for a beneficial effect of nocturnal sleep.

Materials and methods

Our study was approved by the Ethics Committee of the Academic Hospital and Faculty of Medicine of the University of Liège, (number B70720071527). The task was created using Matlab version 7.1, with Cogent 2000 (<http://www.vislab.ucl.ac.uk/cgi-bin/CogentGraphics.cgi>). The stimuli were generated by an HP (Hewlett Packard, USA) pavilion dv2000 laptop (Intel Duo Core Processor T5500, 2 GB RAM) and were presented on a Sony (Sony Corporation, Japan) 19-in. monitor, with maximum contrast and a mean luminance of 45 cd/m² and a maximum illuminance of 50 LUX at 50 cm, at a 1024 × 768 pixels resolution and 60 Hz refresh rate. A standard external USB powered 101 keys keyboard (DELL, USA) and an optical two-touch mouse (Logitech, Switzerland) were used to record the subjects' responses.

Task description

The task consisted in discriminating the orientation of a sinusoidal grating (2 cycles/degree grating, 2° in diameter) placed at 5° eccentricity in the lower right visual quadrant (Figure 1). Its orientation varied randomly between two orthogonal angles (22°5' and 112°5' from horizontal, respectively, referred to "left" or "right" by the subjects) presented in equal proportion. The phases of the gratings were randomized across trials to make sure that subjects discriminated orientation instead of local luminance cues. The stimuli were embedded in a background sinusoidal noise covering the entire screen (i.e., ~9° of the subjects' visual field). Central fixation was enforced by a simultaneous letter discrimination task in which subjects were presented randomly with either the letter "L" or "T" (~1°) at the foveal position. The sequence of a trial was as follows: The background noise was presented for 500 ms after which the stimuli (peripheral grating and central

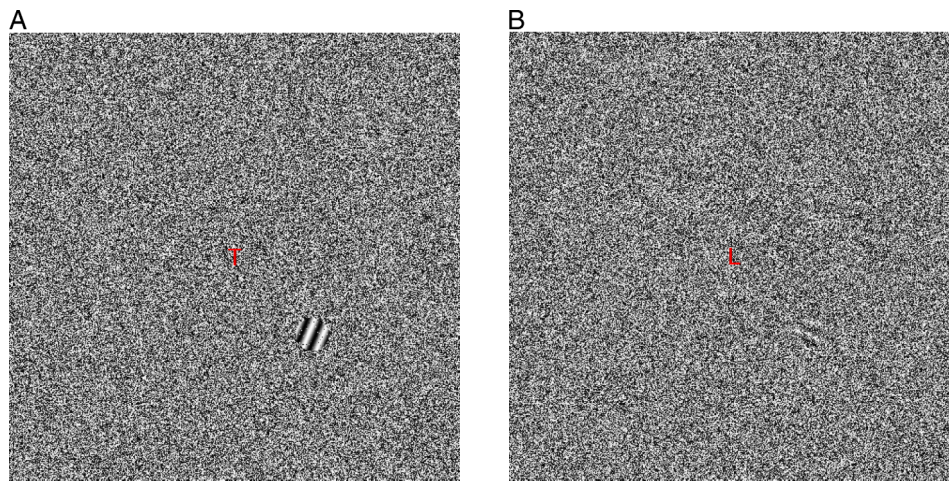


Figure 1. (A) Typical stimulus with the 112.5° orientation, 90% SNR. (B) Typical stimulus, 22.5° orientation, 30% SNR.

letter) and the background noise were displayed for 100 ms, immediately followed by a different background noise covering the entire screen for 500 ms. A prompt was then overlaid on this background, encouraging subjects to give two serial answers pertaining to letter and orientation discriminations, respectively. Subjects were allowed to respond within 3 seconds after probe onset. Only the right and the left directional keys of a standard keyboard were used to respond for both letter and orientation tasks to minimize the subject's distraction resulting from two different sets of keys (L and 22.5° = left key; T and 112.5° = right key). The next trial started as soon as the second answer was given. Subjects were in fact always presented with background noise, the levels of visible signal varying with respect to their answers (Figure 2).

The noise level that partially occluded the grating was adapted to subjects' performance following a 4/1 transformed Up–Down staircase procedure (Wetherill & Levitt, 1965). The noise that partially occluded the grating was sinusoidal matching the luminance distribution of the sinusoidal grating and background. The initial amount of noise occluding the grating started for each session at 10%, corresponding to a signal-to-noise ratio (SNR) of 0.9. For an X SNR ratio, $(1 - X) * 100\%$ grating pixels were replaced by the noise pattern (e.g., for the 0.9 SNR, 10% of the grating pixels were partially occluded by the noise pattern). After 4 consecutive correct orientation discrimination answers, the current SNR was reduced by 6%, whereas it was increased by 6% in case of a single wrong orientation answer. For both experiments, we computed the geometric mean of the SNR value of the reversal points for each block of 100 trials. No auditory or visual feedback was given.

Subjects were placed in a dark room, their head on a head holder, centering their visual field onto the center of the computer monitor. Stimuli were presented at a 50-cm distance from the subject's eye. Single sessions consisted of 5 (Experiment 1) or 10 (Experiment 2) blocks of 100

trials. Each block was manually started by the subjects, allowing them to modulate the length of the pauses between blocks in order to prevent fatigue. Statistical analyses were performed by Statistica 7.1 (Statsoft, USA). Statistical testing was conducted using a Type 1 error of $p < 0.05$.

Experiment 1: Position and orientation specificity

Eleven subjects were recruited for this protocol. A semistructured interview established the absence of

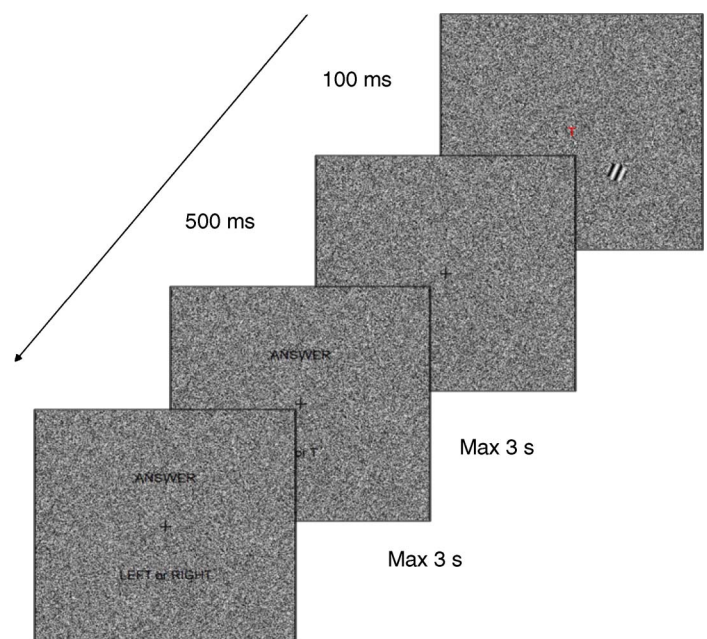


Figure 2. Timeline of a single trial: grating presentation, new background-filled fixation screen, letter answer screen, orientation answer screen.

medical, traumatic, psychiatric history, or of sleep disorders. All participants were non-smokers, moderate caffeine, and alcohol consumers. None were on medication. All subjects signed an informed consent form. Subjects were instructed to follow a regular sleeping rhythm and were not allowed daytime naps; their schedule was checked by a sleep agenda during the week before the first session. Subjects' activity was continuously monitored by actigraphy (Actiwatch, Cambridge Technology, UK) during the whole duration of the study. Each subject was submitted to a daily practice session during 7 consecutive days. Sessions started always at the same time of the day, varying from subject to subject, between 2 and 4 o'clock in the afternoon. Each session consisted of 5 blocks of 100 trials. On day 1 and 7, two tasks were added for a further 5 blocks of 100 trials each. The first additional task consisted of the original coarse orientation discrimination, but testing different orientations (67.5° versus 157.5°). The second task consisted of another 5 blocks of 100 trials in which the same orientations as in the original task were presented in the lower *left* quadrant of the visual field at the mirror location of the trained stimulus at the same eccentricity. In these sessions, subjects performed the 3 tasks consecutively, with pauses consisting in 2-minute breaks in a normally lit room between sessions. The control tests were always performed first, but their order was balanced across subjects.

Statistical analyses consisted in a repeated measurement ANOVA with individual blocks and sessions as within-subjects factors.

Experiment 2: Effect of time and sleep on visual skill learning

Two groups ($N = 14$) of healthy volunteers were recruited using the same criteria as for the first study. In addition, none had worked on night shifts during the last year or traveled through more than one time zone during the last 2 months. Subjects with irregular sleep rhythms and sleep disorders as well as subjects who were not naive to orientation discrimination tasks were not included. All subjects had normal, non-corrected vision. Participants had to fill in a sleep agenda, starting a week before their first session; no naps were allowed between the morning and night sessions.

Each subject performed the task three times, consisting of 10 blocks of 100 stimuli, with a 12-hour interval between each session. Group 1 (morning–evening–morning or MEM) subjects had a first session in the morning at a previously scheduled time (8:00, 9:00, or 10:00), a second one the same night, exactly 12 hours later, and the last one the following morning after another 12 hours delay. Group 2 (evening–morning–evening or EME) subjects started with an evening training at a fixed time (20:00, 21:00, or 22:00) were tested the next morning after

exactly 12 hours and then retested the following evening, again after 12 hours. Statistical analyses consisted in a repeated measurement ANOVA with individual blocks and sessions as within-subjects factors and groups (EME and MEM) as between-subjects factor.

Results

Experiment 1: Position and orientation specificity of coarse orientation discrimination learning

Demographic data

Participants (6 women and 5 men, mean age 22.12 ± 1.2 years) reported to have slept an average of 8 hours and 11 minutes (± 12 minutes) during the 7 days before the first training session. During the experimental week, average sleep time was estimated at 8 hours and 22 minutes (± 27 minutes) based on actigraphic recordings.

Behavioral results

Performance for the trained orientations and position improved from session to session ($16.17 \pm 5.2\%$ SNR decrease from session 1 to session 7; see Figure 3). Subjects quickly reached a plateau level after the first block and remained stable throughout the four last blocks during each session. A repeated measures ANOVA using blocks and sessions as within-subject factors showed a significant effect of the 4 last blocks ($F(3,30) = 6.30$,

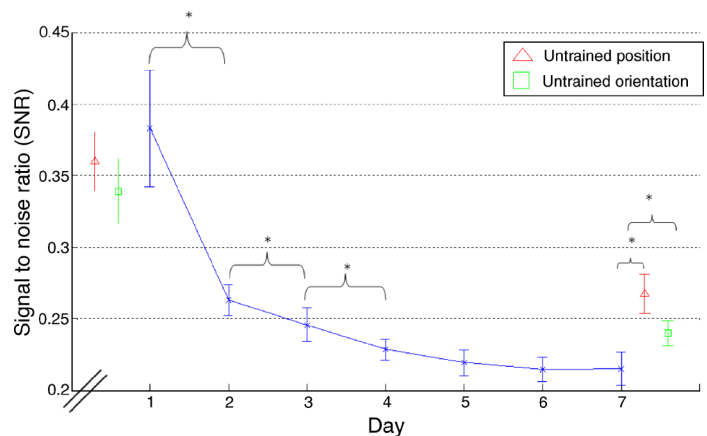


Figure 3. Mean daily performance across sessions. SNR steadily decreases from session to session for the trained orientation and position (blue line). Untrained position and orientation also improve between the first and the last sessions. Notice that the performance on day 7 for these untrained tasks is comparable to performance on day 2 for the trained stimuli. Subjects improved statistically more at trained task than the untrained ones. Error bars indicate standard error of the mean. Note: $*p < 0.05$. $N = 11$.

$p = 0.001$), indicating a within session improvement in performance. There was also a significant main effect of sessions ($F(6,60) = 21.74, p < 0.001$). Planned comparisons showed a statistically significant improvement between sessions 1 and 2 ($F(1,10) = 13.33, p = 0.0044$), 2 and 3 ($F(1,10) = 16.02, p = 0.0025$), and 3 and 4 ($F(1,10) = 5.80, p = 0.036$) but not for later sessions. The improvement in performance across the first three sessions (1 to 3) was significantly greater than the one across the last three sessions (5 to 7, $F(1,10) = 43.86, p < 0.001$). The letter task performance, on the other hand, did not improve significantly from session to session ($F(6,60) = 2.19, p = 0.06$) nor differed between different tasks ($F(1,10) = 3.1, p = 0.10$).

A repeated-measure three-way ANOVA compared performance achieved for the trained and untrained quadrants, using the stimulus location (trained versus untrained quadrant), the sessions (day one versus seven), and the blocks as factors (Figure 4). The main effect of location was not statistically significant ($F(1,10) = 0.48, p = 0.50$). In contrast, the main effect of sessions ($F(1,10) = 24.38, p < 0.001$) and the location by session interaction effect were statistically significant ($F(1,10) = 6.48, p = 0.028$). Planned comparisons showed that performance improved for the trained task between sessions 1 and 7 ($F(1,10) = 11.95, p = 0.006$).

No differences in discrimination were found between trained and untrained quadrants during the initial training session ($F(1,10) = 0.51, p = 0.48$), whereas a significantly lower SNR was achieved for the trained quadrant, compared to the untrained quadrant, on the last training session (day 7, $F(1,10) = 10.12, p = 0.009$).

A repeated-measure three-way ANOVA compared performance achieved for the trained and untrained orientations, using the stimulus orientation (trained versus untrained orientation), the sessions (day one versus seven), and the blocks as factors (Figure 5). The

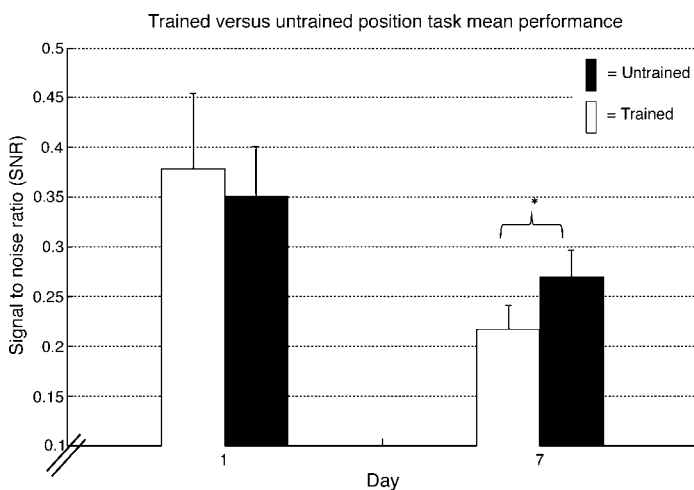


Figure 4. Trained versus untrained position quadrant task performance. Note: $*p < 0.0001$. $N = 11$.

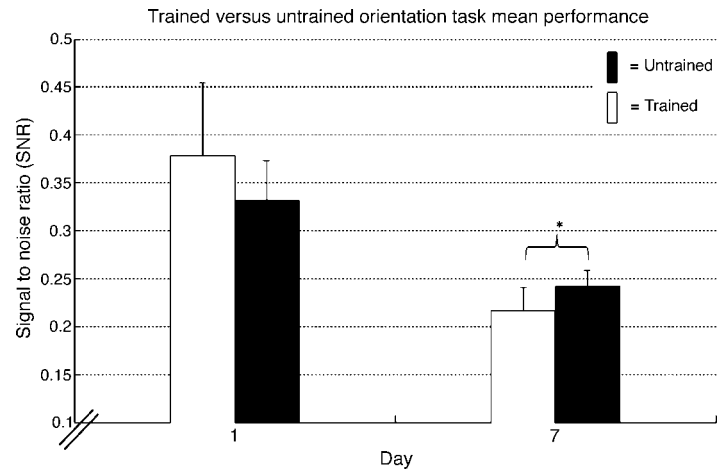


Figure 5. Trained versus untrained orientations task performance. For both figures' control tasks, note the large, unspecific gain between sessions 1 and 7 and the small, specific gain within the different tasks on day 7. Note: $*p < 0.0001$. $N = 11$.

main effect of orientation was not statistically significant ($F(1,10) = 0.12, p = 0.73$), in contrast to the main effect of session ($F(1,10) = 29.92, p < 0.001$). The orientation by session interaction in this case was not statistically significant ($F(1,10) = 1.57, p = 0.23$). This is perhaps due to the fact that the sensitivity to the trained orientation progressively emerged through repeated training. Indeed, planned comparisons showed that no differences were found between trained and untrained orientations during the initial training ($F(1,10) = 0.65, p = 0.43$). However, subjects improved for the untrained orientations between sessions 1 and 7 ($F(1,10) = 25.22, p < 0.001$). Eventually, their performance in the untrained orientations task were not as improved on day 7 as the ones for the trained orientations ($F(1,10) = 30.46, p < 0.001$).

Experiment 2: Effect of time and sleep on coarse orientation discrimination learning

Demographic data

Participants (20 women, 8 men, mean age 22.64 ± 1.2 years) reported to have slept a mean of 8 hours and 4 minutes (± 12 minutes) during the 7 nights before the first learning session. The average estimated sleep time on the post-training night, based on actigraphic recordings, was 8 hours and 8 minutes (± 11 minutes). There was no significant difference between the EME and the MEM groups neither in reported sleep before the experiment nor in activity during the post-training night. We excluded from our analyses subjects whose performance was worse than the mean plus three times the standard deviation across subjects. Twelve and eleven subjects were eventually included in EME and MEM groups for the analyses.

Behavioral results

Results are displayed in Figure 6. A repeated-measures ANOVA tested for the effects of groups, sessions, and blocks. Only the last six blocks of each session, during which a plateau-like performance was observed, were included in the analysis. The effects of blocks ($F(5,105) = 4.40$, $p = 0.001$) and sessions ($F(2,42) = 23.20$, $p < 0.001$) were significant whereas the group effect was not ($F(1,21) = 0.41$, $p = 0.52$). Planned comparisons showed that SNR in both groups decreased from training to test ($F(1,21) = 10.13$, $p = 0.0044$), from test to retest ($F(1,21) = 12.13$, $p = 0.0022$), as well as from training to retest ($F(1,21) = 50.09$, $p < 0.001$). The session by block interaction was significant ($F(10,210) = 1.97$, $p = 0.037$), indicating that the change in SNR from block to block differed between sessions. Indeed, the mean change in SNR was larger during the first than subsequent sessions, averaged across the groups ($F(1,21) = 38.80$, $p < 0.001$). Typically, during the first session SNR decreased during the first five blocks before stabilizing at a steady level.

The session by group interactions was significant ($F(2,42) = 3.44$, $p = 0.041$). Planned comparisons showed that in either group, the improvement was statistically significant only after a full night's sleep. Performance was improved more in group EME than group MEM between training and the 1st testing ($F(1,21) = 4.84$, $p = 0.039$), whereas performance improved more in group MEM than EME from testing to retesting sessions ($F(1,21) = 4.9$, $p = 0.036$). The significant improvement shown in group MEM between test and retest was not present between training and test ($F(1,21) = 0.4619$, $p = 0.5041$), even though the time interval was the same, but without a period of sleep in-between. In the same way, the

significant improvement shown in group EME between training and test was not present between test and retest ($F(1,21) = 0.8190$, $p = 0.3757$).

We also checked for SNR differences between groups within each separate session. There was no difference in performance between groups in session 1 ($F(1,21) = 0.08$, $p = 0.77$), suggesting that initial performance was similar irrespective of whether training took place in the morning or in the evening. Performance was better in group EME than MEM during session 2, although the difference was not significantly different ($F(1,21) = 2.23$, $p = 0.15$). Finally, in session 3, performances for both groups were practically identical ($F(1,21) = 0.011$, $p = 0.91$).

To further characterize the effect of offline memory processing, without any confounding practice effect, we performed a complementary repeated measures ANOVA comparing the last two blocks of sessions 1 and 2 (blocks 9 and 10) with the first two blocks of the subsequent practice sessions 2 and 3 (blocks 5 and 6). We found a statistically significant session–group interaction for the training and test sessions ($F(1,22) = 6.32$, $p = 0.035$) and for the test and retest ($F(1,21) = 6.18$, $p = 0.021$).

Finally, we looked for a fast learning phase typically observed during early procedural learning. A repeated measures ANOVA with block repetition (blocks 2 to 10) as within subjects factor, conducted on both groups of subjects, confirmed a significant main effect of blocks ($F(8,134) = 8.37$, $p < 0.001$), indicating a fast improvement in performance during the initial training session.

Importantly, no significant training effect was present for the letter task. Using the mean correct letter answers of the last six blocks of each session, and the same within and between factors as when analyzing the orientation responses, we performed a repeated measures ANOVA.

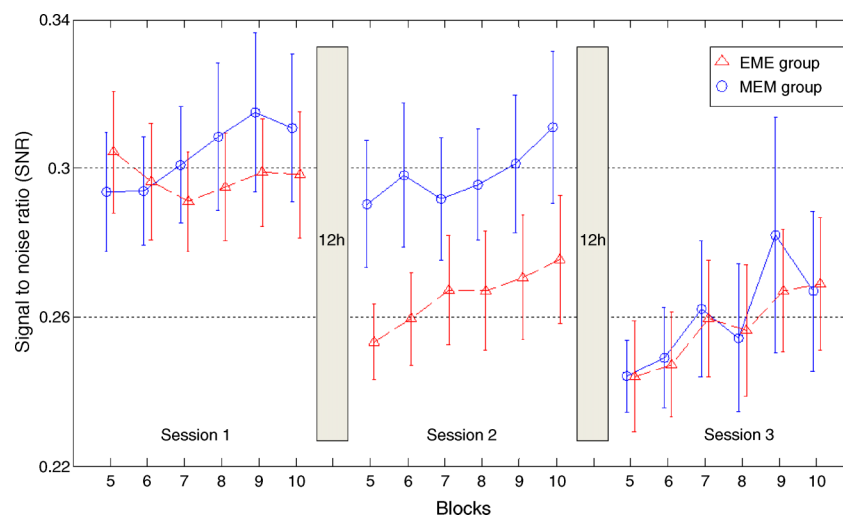


Figure 6. Signal-to-noise ratio for every blocks of the 3 practice sessions. Notice that the improvement in performance is always statistically significant following a night's sleep (that is between sessions 1 and 2 for group EME and between sessions 2 and 3 for group MEM). Error bars represent the standard error of the mean. EME = evening–morning–evening; MEM = morning–evening–morning.

We found no significant main effects and no significant interactions. In particular, session per group interaction was not statistically significant ($F(2,42) = 1.16, p = 0.32$), nor were the main effects of groups ($F(1,21) = 1.51, p = 0.23$), sessions ($F(2,42) = 0.558, p = 0.57$), or blocks ($F(5,105) = 0.3877, p = 0.85$).

Discussion

We used a coarse orientation discrimination task to investigate offline memory processing taking place between sessions during both wakefulness and nocturnal sleep. Our main results are threefold. First, performance in a coarse orientation discrimination task improves with practice. Second, this visual learning depends on orientation and is retinotopic. This suggests that learning this visual skill involves selective populations of orientation-specific neurons. Third, the visual skill learning curve includes an initial fast learning phase within the first training session and a slow learning phase between subsequent practice sessions. The latter suggests that visual skill is reprocessed offline. We further provided evidence that these offline processes are associated with larger gains in performance if they take place during sleep rather than during wakefulness. This kind of sleep-related improvement is potentially specific to visual tasks. The available evidence suggests for instance that auditory perceptual learning improves with time and not necessarily in relation to sleep (Gottselig et al., 2004; Roth, Kishon-Rabin, Hildesheimer, & Karni, 2005).

Perceptual skill learning followed an asymptotic learning curve at two different temporal scales: across blocks during the initial training session and across sessions in the course of repeated daily practice. During the initial training session, performance considerably increased during the first blocks before stabilizing after a few practice blocks (Experiment 2). This time course is reminiscent of the fast learning phase reported in procedural motor skill learning (Karni et al., 1998). In addition, with repeated daily practice over a week (Experiment 1), visual skill improved between the first sessions before reaching an asymptote during which no additional gain in performance is observed between sessions. This second phase, referred to a “slow learning” phase in motor learning, has been related to distinct plastic changes within the primary motor cortex in the case of motor learning (Karni et al., 1998). It is not yet known if performance could be further improved by longer lasting training periods nor if the visual skill is retained for time intervals of months or years.

An important finding is that discrimination performance improves *between* sessions, suggesting that neural representations underpinning the novel visual skill are

processed offline without practicing the task. This offline processing progressively develops but time is not the only factor that explains the gain in performance between sessions. Although performance improves both over the day and overnight, the gain in performance is significantly larger after a night of sleep than after the same time interval spent awake (i.e., between training and testing in EME subjects and between test and retest sessions in MEM subjects). These findings are consistent with a favorable effect of sleep on the consolidation of visual perceptual skills. Alternatively, memory consolidation might be influenced by a circadian process (Cajochen et al., 2004), which would specifically take place during the night. Although such an effect cannot be ruled out, it is to note that no circadian effect was observed on performance since the same discrimination levels were measured during training and retest sessions that were scheduled during the evening (EME) or the morning (MEM). Future experiments probing the effects of diurnal sleep (i.e., naps) on coarse orientation discrimination should specifically confirm a beneficial effect of sleep on this visual skill learning.

The emerging visual skill was specific to the trained quadrant and orientation (Experiment 1). After 7 daily training sessions, the SNR achieved for the trained orientations was significantly lower than for 2 untrained orthogonal orientations. This finding suggests that orientation-selective neural populations underpin the new visual skill. These neural ensembles may be located in early visual areas V1 and V4, which are known to be brain areas representing orientation specificity (Hubel & Wiesel, 1968; McAdams & Maunsell, 1999; Raiguel, Vogels, Mysore, & Orban, 2006; Schiller & Stryker, 1972; Tootell et al., 1998). Likewise, the SNR achieved after 7 days of training for the trained quadrant was significantly lower than for the contra-lateral quadrant. This result indicates that the acquired visual skill is specific to the position of retinal input associated with the target grating, suggesting a retinotopic mapping of learning-related changes in responses of early visual areas.

Conclusions

The offline learning of PL has been extensively studied using the TDT. Our results confirm and extend this body of evidence by generalizing it to a coarse orientation discrimination task. Initial practice is associated with a fast within-session improvement in discriminative abilities. Subsequently, performance continues to improve between practice sessions, suggesting an offline processing of the perceptual memory. These performance gains are specific to the trained orientations and locations. They are larger after a night of sleep than after the same time interval spent awake, suggesting a beneficial effect of nocturnal sleep.

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