

Two phases of offline learning in contour integration

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We demonstrate daytime and overnight offline modulations of perceptual learning in a visual integration task. We employed a contour integration task, which requires longer range spatial integration than the more commonly used texture discrimination task, yet, still addresses the earliest cortical processing levels. In order to dissociate the effect of daytime and overnight offline modulations on perceptual learning, we introduced a 12-h shift between the practice times of two groups of subjects. Throughout the five practice sessions, the 12-h shift resulted in stepwise modulation of a typical learning curve, with a phase shift between the two groups. Between sessions (offline) improvement during the day was relatively small and only occurred in the first few sessions, while it was always significant after a night of sleep. Our results extend the body of evidence on the potential role of sleep in perceptual learning and generalize it to integrative visual processes. We have clearly distinguished two phases of learning: both daytime and overnight improvements in the initial phase, and only overnight improvements in the later phase.

Keywords: sleep, learning, perceptual learning, visual integration, contour integration

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Introduction

Repeated exposure to sensory experience results in enhanced performance in perceptual tasks and plastic reorganization even in the adult brain (e.g., Karni & Sagi, 1991; Schwartz, Maquet, & Frith, 2002). With respect to visual perceptual learning, sleep dependence has been studied extensively in a texture discrimination paradigm (Gais, Plihal, Wagner, & Born, 2000; Karni, Tanne, Rubenstein, Askenasy, & Sagi, 1994; Stickgold, Whidbee, Schirmer, Patel, & Hobson, 2000) and, more recently, with respect to orientation discrimination (Matarazzo, Frankó, Maquet, & Vogels, 2008). Visual contour integration involves spatial integration at a longer range than texture or orientation discrimination; however, it still relies on early visual processes such as long-range interactions between orientation-selective neurons in the primary visual cortex (e.g., Giersch, Humphreys, Boucart, & Kovács, 2000; Kovács, 1996; Kovács & Julesz, 1993; for neural correlates, see, e.g., Altmann, Bulthoff, & Kourtzi, 2003; Kourtzi, Tolias, Altmann, Augath, & Logothetis, 2003; with respect to the low-level nature of this task, also see the first paragraph of the Discussion section). Perceptual learning has been demonstrated earlier in contour integration (Kovács, Kozma, Fehér, & Benedek, 1999; Kozma,

Kovács, & Fehér, 2002), and it was found to be specific to stimulus features (Kovács et al., 1999). Cue independence of learning indicates that it is related to early visual processing, possibly involving use-dependent changes in connectivity within the orientation-selective neuronal populations in the primary visual area. The well-defined nature of learning in the contour integration task promises that it might become a good model of memory consolidation in more general terms and motivates the question whether—similarly to improvements in texture or orientation discrimination—it is sleep-dependent or not. Our aim here is to clarify the modulatory role of both daytime and nighttime offline learning in contour integration.

In terms of methodology, sleep deprivation is a standard behavioral method to confirm the role of sleep in perceptual learning (Karni et al., 1994; Stickgold, James, & Hobson, 2000). However, it is equivocal whether the deterioration in performance is purely due to the lack of sleep (or certain sleep phases) or to other confounding factors such as fatigue, reduced attention, etc. The daytime nap paradigm has been introduced by Mednick, Nakayama, and Stickgold (2003) to control for many confounds of sleep studies. Another approach is to vary the time distribution of training sessions: for example, one group of subjects practices within the same day, while the practice sessions of the other group are distributed into two or

more consecutive days (Kozma et al., 2002). The flaw in this design is that it does not allow for the distinction between time- vs. sleep-dependent learning. In order to avoid the above-mentioned confounding factors, we employ a 12-h shift design (see Figure 1b and the Methods section) that was developed earlier to test motor skill learning by Walker, Brakefield, Morgan, Hobson, and Stickgold (2002) and introduced to visual learning by Mednick, Drummond, Boynton, Awh, and Serences (2008) and Matarazzo et al. (2008) more recently. By applying a larger number of sessions, this design is useful not only in terms of investigating the sleep dependency of learning, but it might help isolate purely sleep-dependent performance enhancement from other more mixed stages of perceptual learning, such as an initial phase, where higher level cognitive and attentional factors play a role. In the 12-h shift design, we expect that the typical learning curve

(Figure 1a) will be modulated by alternating phases of practice, where only every second practice session is followed by a night (Figure 1b). However, as sleep is not the sole determining factor of learning, we expect that the typically continuous learning curve, shown in Figure 1a, will be modulated by the step functions shown in Figure 1b with a phase shift. Introducing a 12-h shift between the first sessions of the two tested groups allows us to clarify whether daytime and nighttime offline learning modulates performance similarly or not.

Methods

Forty university students (22 males, 18 females; mean age = 20.8 years) participated in this study. All observers

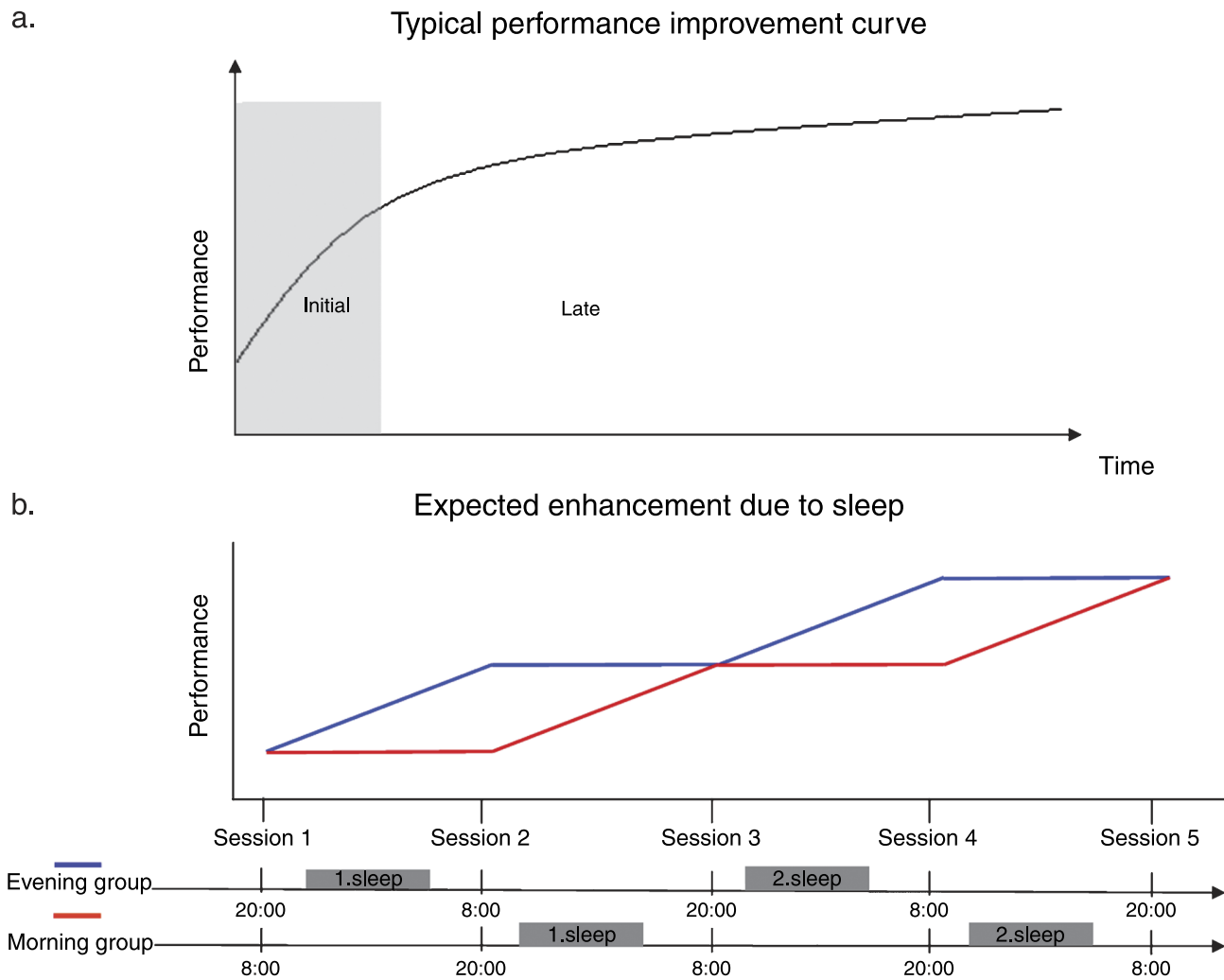


Figure 1. Expected learning curves in the 12-h shift design. (a) The initial phase of learning is usually faster in perceptual learning, resulting in the steeper part of the curve (after Karni & Sagi, 1993). (b) Sessions are shifted by 12 h in the two tested groups (MG: Morning Group, starting at 8:00 AM; EG: Evening Group, starting at 20:00 PM). Both groups are tested every 12 h. By the 2nd and 4th sessions, the EG group has one more night of sleep than the MG group. The blue (EG) and red (MG) curves represent the anticipated performance improvement due to sleep.

had normal or corrected-to-normal vision and had no history of neurological illness or sleep disturbance. Participants were randomly assigned to two groups (Morning Group (MG), $n = 20$, 11 males, 9 females; mean age = 21.7 years; or Evening Group (EG), $n = 20$, 11 males, 9 females; mean age = 20.7 years; see later) and were naive to the purpose of the study. In order to rule out the confounding effects of chronic sleep restriction, and possible daytime sleep, we asked our subjects to report the amount of both night- and daytime sleep preceding every training session. Less than 6 h nighttime sleep or a reported daytime nap of any length were excluding factors even if the subject completed a number of training sessions already. During the course of the experiment, we excluded 7 subjects because of less than 6 h sleep, and 2 subjects because they reported a daytime nap. We replaced the excluded subjects with new subjects in order to keep 20 subjects in each experimental group.

Stimuli were composed of closed contours against noisy backgrounds (see, e.g., Kovács & Julesz, 1993; Kozma-Wiebe et al., 2006). The target was a collinear chain of Gabor elements forming a horizontally oriented egg shape with its narrower part pointing either to the right or to the left. The egg-shaped contour was embedded in a background of randomly positioned and oriented Gabor patches. The carrier spatial frequency of the Gabor patches was 5 c/deg and their contrast was 95%. The spacing between the contour elements was kept constant (8λ ; where λ is the wavelength of the Gabor stimulus). The signal-to-noise ratio as defined by a D parameter ($D = \text{average background spacing/contour spacing}$) of each image was 0.9. By keeping D at a constant level below 1.0 ($D = 0.9$), subjects' performance is a function of the adequacy of

long-range interactions between orientation-selective neurons in the primary visual cortex (see, e.g., Kovács, 1996). The orientation jitter of the contour elements was varied between 0° and 24° across six difficulty levels (0° , 8° , 12° , 16° , 20° , 24° , see Figure 2). A set of 40 images was presented in 4 blocks of 10 trials at each of the six difficulty levels in each session. One session of 240 trials lasted about 20 min. A new shape and background were generated for each stimulus, but all of the contours had the same general size and egg-like shape.

The blocks of images were presented in a two-alternative forced-choice (2AFC) procedure, in an increasing order of difficulty, starting with the easiest (0° orientation jitter) level, and followed by more and more difficult (8° , 12° , 16° , 20° , 24° orientation jitter) levels. Stimulus duration was 2 s, with a fixation cross between stimuli (0.5 s, or until the subject responded). Subjects had to indicate which side of the screen the narrower part of the egg was pointing to. Subjects were tested binocularly and were seated at about 0.4 m away from a 17-in. HP monitor in a normally lit testing room. Monitor resolution was set to 1280×1024 . Images subtended 19.93° of visual angle vertically and 26.57° of visual angle horizontally from the testing distance. The mean luminance of the monitor was 21.5 cd/m^2 .

Psychometric functions for each subject were plotted using mean scores for each of the six levels of jitter, and threshold performance was calculated by fitting a Weibull function on the data points. Threshold was defined by orientation jitter at 75% correct performance.

We introduced a 12-h shift between the two groups of subjects. Each participant practiced in the contour integration task five times within 2 and a half days. MG subjects

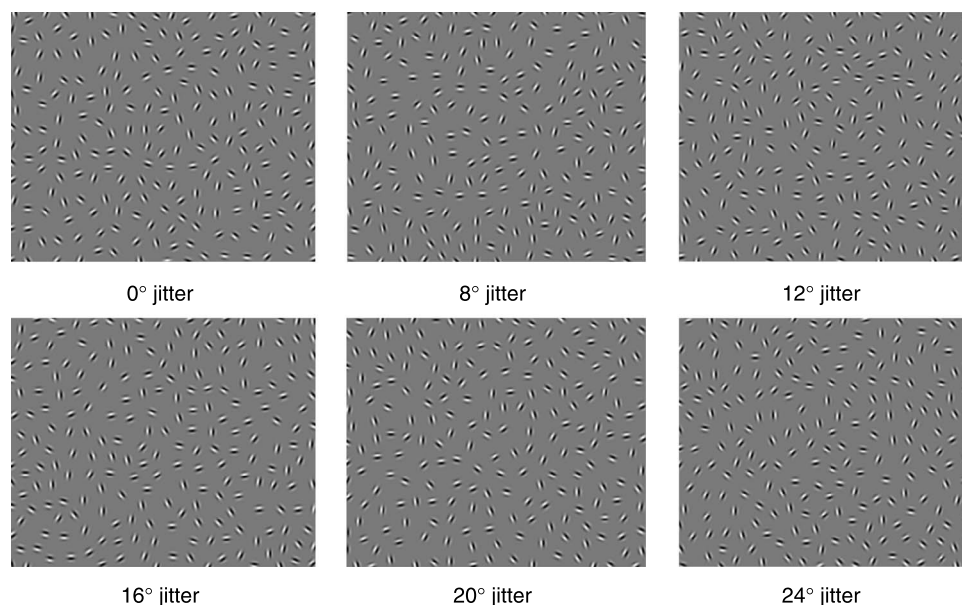


Figure 2. Stimuli. There is a collinear chain of Gabor elements forming a horizontally placed egg shape on a background of randomly positioned and oriented Gabor patches within each panel. The orientation of contour elements was jittered from the original path of the contour allowing for six difficulty levels, as shown in the individual panels.

started the first session at 8:00 AM, while EG subjects started at 20:00 PM on the same day (see Figure 1b). By the second and fourth sessions, the groups had different amounts of night sleep, but other factors (number of trials, time between sessions, etc.) were equivalent.

It is relevant to mention that, compared to earlier studies, here we increase the number of sessions. That might augment the offline effects of sleep in the later sessions where those are not confounded by the initial boost of performance observed both in perceptual and motor learning (Hotermans, Peigneux, Maertens de Noordhout, Moonen, & Maquet, 2006; Karni et al, 1994).

Results

Evening group

Between Session 1 and Session 2, EG showed significant performance enhancement (1.44° ; paired t -test: $t = -6.94$, $df = 19$, $p < 0.001$). Statistically significant but smaller improvement (0.6° ; paired sample t -test: $t = -2.46$, $df = 19$, $p = 0.023$) was present between Session 2 and Session 3. Between Session 3 and Session 4, the group continued to improve significantly (1.9° ; paired sample t -test: $t = -6.82$, $df = 19$, $p < 0.001$). EG performance

did not change between Session 4 and Session 5 (paired sample t -test: $t = 1.15$, $df = 19$, $p = 0.263$; see Figure 3).

Morning group

Between Session 1 and Session 2, MG improved significantly (0.7° ; paired t -test: $t = -3.52$, $df = 19$, $p = 0.002$). A more substantial enhancement was found between Session 2 and Session 3 (1.3° , paired sample t -test: $t = -8.46$, $df = 19$, $p < 0.001$). MG presented no enhancement between Session 3 and Session 4 (paired t -test: $t = -0.04$, $df = 19$, $p = 0.963$) but improved significantly between Session 4 and Session 5 (1.7° , paired sample t -test: $t = -7.34$, $df = 19$, $p < 0.001$).

Intergroup differences

Initial (Session 1) performance was the same in the two groups (EG = 13.4° , $SD = 0.71$; MG = 13.46° , $SD = 0.96$; independent-groups t -test: $t = -0.237$, $df = 38$, $p = 0.812$). However, in Session 2, EG performed significantly better than MG (EG = 14.84° , $SD = 0.87$; MG = 14.13° , $SD = 1.2$, independent-groups t -test: $t = 2.12$, $df = 38$, $p = 0.04$). Performance was very similar in the two groups in Session 3 again (EG = 15.47° , $SD = 1.7$ and MG = 15.44° , $SD = 1.36$;

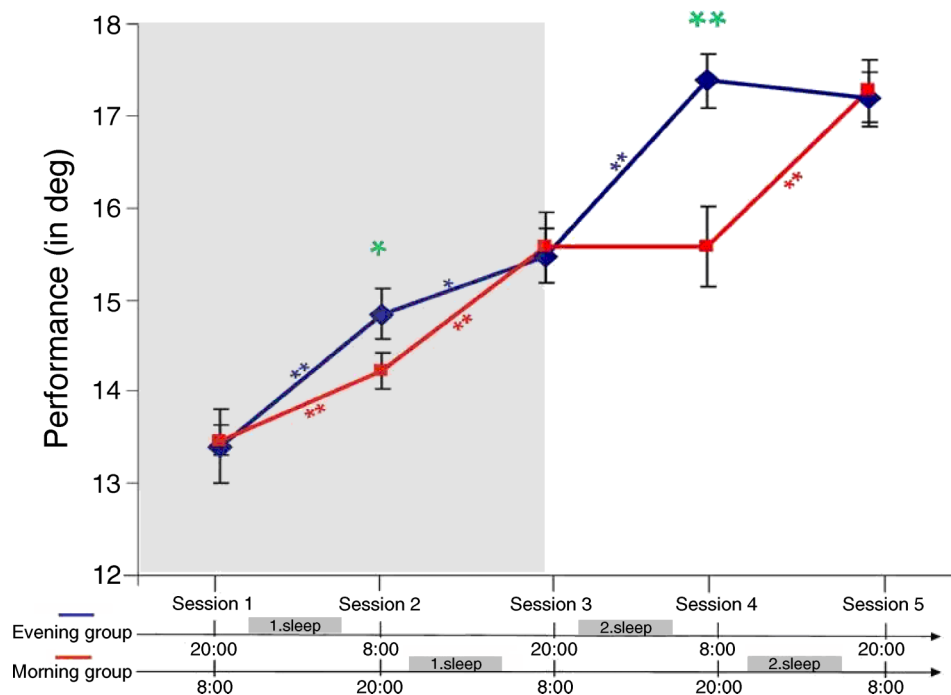


Figure 3. Learning curves in the 12-h shift design (red: MG, blue: EG). Performance of each group in the five practice sessions (horizontal axis) is presented as the maximal orientation jitter at threshold (vertical axis) in the contour integration task. The 12-h shift resulted in a stepwise modulation of the typical learning curve (as predicted in Figure 1a), with a phase shift between the two groups, clearly indicating a strong modulatory effect of nighttime offline learning. Daytime learning is only observed in the first few sessions (shaded box), while overnight learning is more pronounced in the later ones.

independent t -test: $t = -0.168$, $df = 38$, $p = 0.78$). In Session 4, EG performed significantly better (EG = 17.37° , $SD = 1.93$; MG = 15.45° , $SD = 36$; independent t -test, $t = 3.62$, $df = 38$, $p = 0.001$), and the difference between the two groups was more remarkable than in Session 2. Final performance in Session 5 was very similar again (EG = 17.18° , $SD = 1.56$; MG = 17.16° , $SD = 1.33$; independent t -test: $t = 0.038$, $df = 38$, $p = 0.97$).

Note that significant intergroup difference was present only in Session 2 and Session 4, where the groups had a different amount of sleep. In case of all the other sessions, the groups had the same amount of sleep and there was no significant difference in their performance.

A repeated-measures two-way ANOVA compared the performance of the two groups (MG/EG) in the five sessions. The effect of group was not significant ($F(1, 38) = 2.47$, n.s.), in other words, overall performance, and improvement of the two groups, disregarding the 12-h shift, was the same. The effect of session was significant ($F(1, 38) = 98.77$, $p < 0.01$), a consistent session by session improvement was present. Group by session interactions were revealed by a post hoc analysis and were significant in Session 2 ($F(1, 38) = 4.5$, $p < 0.05$) and Session 4 ($F(1, 38) = 13.14$, $p < 0.05$), as the green asterisks also indicate that in Figure 3, based on the results of the paired t -tests.

A three-way repeated-measures ANOVA tested for the effects of group (MG/EG), learning phase (*initial phase*: improvements between Session 1 and 2, and Session 2 and 3; *late phase*: improvements between Session 3 and 4, and Session 4 and 5; the initial phase is indicated by the shaded box in Figure 3), and the effect of sleep (sleep vs. no sleep improvements). The effect of sleep was significant ($F(1, 38) = 110.21$, $p < 0.01$) whereas the effect of group ($F(1, 38) = 0.03$, n.s.) and the effect of learning phase ($F(1, 38) = 1.32$, n.s.) were not. Further analysis revealed that sleep by learning phase interaction was significant ($F(1, 38) = 7.02$, $p < 0.05$), implying that sleep affected performance differently in the two learning phases. The effect of consolidation phase was significant for no sleep improvements ($F(1, 38) = 7.35$, $p < 0.05$), while it had no effect for improvements preceded by sleep ($F(1, 38) = 0.77$, n.s.). In other words, the effect of sleep was always significant, while daytime improvements only occurred in the initial phase (as shown by the results of the paired t -tests in Figure 3 as well).

Discussion

We used a contour integration task to study the effects of sleep and time in perceptual learning. The contour integration task has been developed earlier in order to test the integration properties of neurons with conjoint orientation preference in the primary visual cortex in a behavioral

paradigm (Field, Hayes, & Hess, 1993; Kovács & Julesz, 1993). These stimuli have been designed to specifically address processing in the primary visual cortex. Neural correlates, found more recently, seem to indicate the role of lower level visual areas in integrating the contour-in-noise stimulus as well (Altmann et al., 2003; Giersch et al., 2000; Kourtzi et al., 2003). A possible candidate for assembling local orientation information already within the primary visual cortex is the plexus of long-range horizontal connections (see, e.g., Gilbert & Wiesel, 1992). Cue-specific perceptual learning in the task has been demonstrated earlier. It has been shown that practicing with color- vs. orientation-defined contour stimuli does not transfer across these attributes (Kovács et al., 1999). This cue-specific improvement indicates that learning takes place at an early cortical level, not involving high level, or feedback processes. In this respect, the contour integration task is similar to the frequently used texture discrimination task (Karni & Sagi, 1991) and the more recently developed coarse orientation discrimination task (Matarazzo et al., 2008) that are both employed in studies on sleep-dependent learning. However, the contour integration task requires integration across a large area in the visual field, while performance in the texture and coarse orientation discrimination tasks is based on the output of local filters. The specific type of contour integration stimulus employed in our experiment is also different from the generally used version, where a relatively short, straight, or slightly curved line is embedded in a constant amount of noise (Field et al., 1993; Hess & Field, 1999). Our paradigm allows for adjusting the amount of noise and the shape of the contour. Both of these parameters are important in demonstrating that closed contours are easier to detect in this task than non-closed ones, and that shape-dependent contextual effects are already present at this level of processing (Kovács & Julesz, 1993, 1994; Mathes & Fahle, 2007). The current study, employing the latter type of visual stimuli, addresses the question whether these more global shape-dependent processes are enhanced by offline learning during sleep.

Perceptual learning in the 12-h shift paradigm followed a typical learning curve (Figure 1a) with a stepwise modulation (Figures 1b and 3). The stepwise modulation appeared with a phase shift in the two experimental groups, and it was more enhanced in the last few sessions. The pattern of results unequivocally indicates that night sleep results in the enhancement of performance in the lack of further stimulation or practice, which is consistent with earlier findings in perceptual learning (e.g., Karni & Sagi, 1991; Stickgold, James et al., 2000). Improvement might be a result of use-dependent changes in connectivity within the orientation-selective neuronal populations in the primary visual area.

The 12-h shift paradigm with 5 sessions and 2 experimental groups also provided for a clear distinction between two phases of offline learning. Our results indicate that there is an initial phase of learning, including the first few

sessions, in which relatively smaller but significant daytime improvements also occur in addition to sleep-dependent learning. In the second phase of learning, we only observed overnight improvements. Significant daytime improvements were also observed in texture discrimination, depending on the number of trials in a single session (e.g., Censor, Karni, & Sagi, 2006) and during the acquisition of skilled motor performance (e.g., Kami et al., 1998; Korman, Raz, Flash, & Karni, 2003; Walker et al., 2003). Such a clear distinction between the “mixed” and “sleep-dependent” phases has not been demonstrated before. There is a possibility that the initial phase involves higher level cognitive and attentional processes, and the second phase is more specific to low-level cortical changes. In future studies, cue specificity of these two phases might clarify this issue.

An alternative scenario is that the two observed phases of learning are different in terms of the level of sensory adaptation present in the low-level visual system. Censor and Sagi (2008, 2009) recently put forward a saturation hypothesis with respect to perceptual learning in texture discrimination. In this framework, overexposure to the stimulus saturates the processing network and results in less efficient processing by strengthening task-irrelevant synapses. They have shown that both daytime and overnight improvements depend on the number of practice trials. In our experiment, there is a possibility that improved performance by Session 3 results in a larger number of visible contours compared to that of Session 1. Theoretically, the “extra” (approximately 40) visible contours might have resulted in a saturation effect, thereby eliminating daytime improvement. Practically, however, such a change in the adaptation state of the network has been induced in the earlier studies (Censor & Sagi, 2008, 2009) by hundreds of “extra” trials. Therefore, we suggest that the difference between the first and second phases of learning is valid in terms of mixed daytime and overnight versus only overnight improvement.

The role of different sleep stages in the two distinguishable phases of perceptual learning of visual integration shall be a topic of further polysomnographic studies.

Conclusions

We distinguished two phases of offline perceptual learning in a visual integration task using a 12-h shift design: both daytime and overnight improvements in the first phase, and only overnight improvements in the second phase.

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