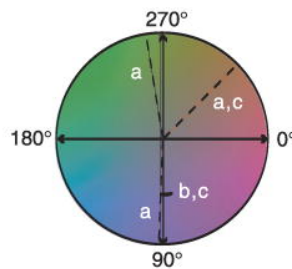


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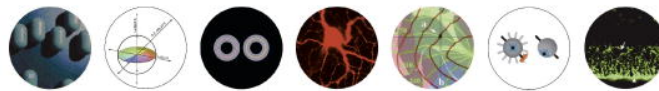


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A link between perceptual learning, adaptation and sleep

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Abstract

Between-sessions gains in the texture discrimination task have been attributed to memory consolidation. A strong dependence of consolidation on sleep was suggested though not always supported by experimental results. Here we suggest that the interaction between consolidation and sleep depends on the adaptation level obtained during the training session. We find that both discrimination thresholds and learning depend on the number of trials used during training, with more trials producing higher discrimination thresholds due to suppressive processes related to adaptation. In addition, while learning benefits from increasing number of trials, a further increase in number of trials reduces learning. Consolidation may benefit from between-session sleep in the adapted states.

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1. Introduction

Perceptual learning refers to improvement in perception which is dependent on practice. Studies using the texture discrimination task showed that latent, slowly evolving between-session improvement in performance often occurs, which is retinotopically-local, orientation-specific and in part monocular, suggesting localized plasticity in human adult primary visual cortex (Karni & Sagi, 1991, 1993; Schwartz, Maquet, & Frith, 2002). These delayed performance gains have been attributed to memory consolidation processes (Karni & Sagi, 1993; Karni, Tanne, Rubenstein, Askenasy, & Sagi, 1994; Stickgold, Whidbee, Schirmer, Patel, & Hobson, 2000; Stickgold, James, & Hobson, 2000).

Other studies using the texture discrimination task (Mednick et al., 2002; Mednick, Arman, & Boynton, 2005; Ofen, Moran, & Sagi, 2004) demonstrated that repeated exposure to the visual task leads to reduced performance which is specific to previously tested regions of

the visual field. Similar patterns of stimulus specificity were found for performance deterioration between sessions separated by a few hours (Mednick et al., 2002, 2005) and within a single session (Ofen et al., 2004), the latter traditionally attributed to visual adaptation. Therefore it was suggested that the deterioration was not just due to general fatigue, but rather because specific neural networks in the primary visual cortex become gradually saturated through repeated testing.

Our current study links, for the first time, the memory consolidation process and the perceptual deterioration (related to adaptation) process. This link may explain differences between the experimental results obtained in previous studies where the role of sleep versus time per-se in memory consolidation is debated. Some studies showed that improvement can occur during daytime without sleep (Karni & Sagi, 1993; Karni et al., 1994) while others found that between-session sleep is required for improvement (Stickgold, James, et al., 2000; Stickgold, Whidbee, et al., 2000; Mednick, Nakayama, & Stickgold, 2003). Considering other visual tasks, learning within a daily session is frequently observed (Fahle, 2004). The current study resolves some of these inconsistencies by demonstrating how different experimental parameters can affect the discrimination

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thresholds and the observed improvement effects in different training and testing conditions. In all the experiments described below, observers were tested in three sessions (Morning 1, Evening, Morning 2), with sleep afforded between the evening and the following morning sessions, as previous results (Karni et al., 1994; Stickgold, Whidbee, et al., 2000) showed no effect of starting time (morning or evening) of practice on the sleep effect. The experiments conducted in this study differed one from the other in the number of trials used in a session.

2. Methods

2.1. Subjects

The subjects were 38 paid high-school or undergraduate students with normal or corrected-to-normal vision.

2.2. Apparatus

The stimuli were presented on a 19 in. Mitsubishi Diamond Pro 930SB color monitor, using a PC with an Intel Pentium processor. The luminance of the stimulus (line textures) was 64 cd/m^2 in an otherwise dark environment.

2.3. Stimuli and procedure

The experimental procedure was similar to that of Karni and Sagi (1991) and Stickgold, Whidbee, et al. (2000), with some differences explained below. We used the standard texture stimuli (40 ms) followed by patterned masks (100 ms). Observers had to decide whether an array of 3 diagonal bars embedded in a background of horizontal bars (19×19 , $0.45^\circ \times 0.03^\circ$ each, and spaced 0.74° apart) was horizontal or vertical. Display size was 14° by 14° of visual angle, viewed from a distance of 100 cm. The target appeared randomly and equally, either in the lower left

or lower right visual quadrant, at 4.46° – 6° of visual angle from center of display. Fixation was enforced by a forced-choice letter-discrimination task, between a “T” and an “L”, at the center of the display. The time-interval between the target stimulus and the mask (stimulus-to-mask onset asynchrony, SOA) was manipulated. After an initial SOA wherein above 90% correct texture discrimination occurred was determined, the SOA was gradually decreased by steps of 20–40 ms (3–4 blocks, with 12–50 trials each, per SOA) to obtain a psychometric curve. Each psychometric curve was fitted with the Weibull function, with an additional finger error parameter $1 - p$, yielding the function:

$$y(t) = p \left\{ 1 - \frac{1}{2} \exp \left[\left(-\frac{t}{T} \right)^\beta \right] \right\} + \frac{1-p}{2} = \frac{1}{2} \left\{ 1 + p \left[1 - \exp \left[\left(-\frac{t}{T} \right)^\beta \right] \right] \right\},$$

where T is the threshold for each curve, defined as the SOA for which 81.6% of responses were correct. In each session, the threshold SOA for the left and right targets was averaged. Sessions were terminated when the subject reached an SOA with close to chance level (defined as less than 65% correct responses) of performance (with the exception of Experiment 1 where nearly half of the subjects were not stopped at close to chance level performance).

3. Results

Experiment 1 included three sessions with blocks containing 50 trials each: a morning session, followed by an evening session 8–10 h later (no sleep allowed) and a third session on the following morning, after a night's sleep. On all sessions following the initial session, the initial SOA was set to the lowest SOA for which at least 85% correct discrimination was obtained in the previous session. All participants ($n = 12$, one excluded because of an initial threshold higher than two standard-deviations from the average initial threshold, Fig. 1a) showed a significant group-average threshold difference between sessions

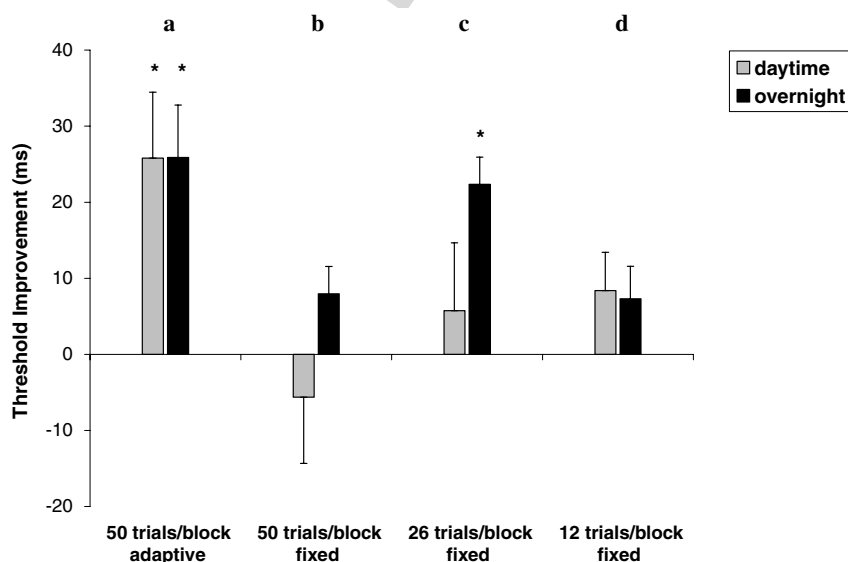


Fig. 1. Group-average threshold improvement for participants during daytime (between the morning and evening sessions) and overnight (between the evening and following morning sessions, including a night of sleep). Asterisks represent significance ($P < .05$) of average improvement: (a) When sessions started at an SOA for which at least 85% correct discrimination was obtained in the previous session (50 trials/block adaptive), a significant threshold decrease was obtained during daytime and after a night of sleep. (b) When all sessions started at the same high SOA (50 trials/block fixed), no significant improvement was obtained between sessions. (c) When the number of trials per block was reduced (26 trials/block fixed), significant threshold improvement was obtained only after a night of sleep. (d) When the number of trials per block was further reduced (12 trials/block fixed), no significant threshold improvements were observed during either daytime or overnight, though a complete 24 h cycle yielded significant improvement (see text).

(repeated measures ANOVA, $p < .0001$). There was a significant decrease in the group-average threshold during daytime between the morning and evening sessions (mean threshold decrease 25.8 ms, SE ± 8.7 ms, paired t -test: $p = .006$). The threshold continued to decrease significantly overnight, between the evening and the following morning sessions (25.9 ± 6.9 ms, $p = .002$). There was no difference in results between participants that were stopped at close to chance level performance and participants that continued to the lower SOAs. This experiment replicated earlier results with a similar method (Karni & Sagi, 1993; Karni et al., 1994).

In experiment 2, the experimental procedure was identical to that of experiment 1, except that the number of trials in the two final sessions was increased by having the participants start with an SOA identical to the one used in the first session i.e., including in both sessions several blocks with nearly perfect performance. There was no significant difference in the group-average threshold ($n = 5$, Fig. 1b) between sessions either overday or overnight (repeated measures ANOVA, $p = .16$).

Experiment 3 was designed to study the relationship between the number of trials afforded in the training session and the obtained threshold. The experimental procedure was identical to that of experiment 2, except that each block contained only 26 trials. This protocol resulted in significant differences in the group-average threshold ($n = 7$, Fig. 1c) between sessions (repeated measures ANOVA, $p < .005$). Altogether, the participants showed a significant morning-to-morning threshold improvement (mean 28.1 ms, SE ± 7.6 ms, paired t -test: $p = .005$). However, there was no significant improvement across daytime (mean 5.7 ms, SE ± 8.9 ms, paired t -test: $p = .27$) but a significant improvement in the group-average threshold overnight (mean 22.4 ms, SE ± 3.6 ms, paired t -test: $p = .0004$). This experiment replicated earlier results with a similar method (Stickgold, James, et al., 2000; Stickgold, Whidbee, et al., 2000).

In experiment 4, the number of trials was further reduced by repeating the experimental procedure of experiments 2 and 3, except that each block was reduced to only 12 trials. In this condition, participants ($n = 7$, Fig. 1d) showed a significant difference in the group-average threshold between sessions (repeated measures ANOVA, $p < .05$). Altogether, there was a significant decrease in the group-average morning-to-morning threshold measurements (mean 15.7 ms, SE ± 3.5 ms, paired t -test: $p = .002$). However, participants failed to show significant group-average threshold improvement between the morning and evening sessions (mean 8.4 ms, SE ± 5 ms, paired t -test: $p = .073$), nor a significant improvement overnight (mean 7.3 ms, SE ± 4.3 ms, paired t -test: $p = .069$).

The effect of the number of trials per block on the obtained SOA threshold was further examined (Fig. 2). The average initial thresholds of the participants trained with 50, 26 and 12 trials per block were significantly different (ANOVA, $p < .001$). The average initial threshold of

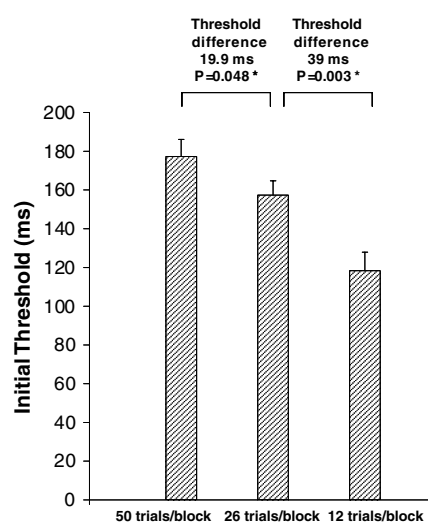


Fig. 2. Comparison between initial thresholds of participants ($n = 17$) performing sessions with 50 trials per block, participants ($n = 13$) performing sessions with 26 trials per block and those ($n = 7$) performing sessions with 12 trials per block. More trials per block resulted in a significantly higher initial threshold.

the participants ($n = 17$) who were given 50 trials per block in each session was significantly higher than the average initial threshold of participants ($n = 13$) that performed sessions with 26 trials per block (mean threshold difference 19.9 ms, t -test: $p = .048$). Moreover, the latter group's average threshold was significantly higher than the average initial threshold of the participants ($n = 7$) that performed sessions with 12 trials per block (mean threshold difference 39 ms, $p = .003$). The increased thresholds with increasing session length found here is consistent with previous results showing performance deterioration as a result of repeated performance of the texture task with closely spaced sessions (Mednick et al., 2002, 2005) or with extended sessions (Ofen et al., 2004).

4. Discussion

The results of experiment 1 of the current study replicated previous studies (Karni & Sagi, 1993; Karni et al., 1994) showing performance gains over-day. In these studies an adaptive method was used and thus the second, evening, session was started at a shorter SOA than the initial morning session. In other studies however (Stickgold, James, et al., 2000; Stickgold, Whidbee, et al., 2000), and in the current experiment 3 gains in performance were found only when sleep was afforded between sessions (sleep-dependent improvements). Such a difference in results can possibly be explained by the dependence of thresholds on number of trials seen in Fig. 2. Shorter sessions produce lower thresholds (see also, Ofen et al., 2004), thus, starting at a shorter SOA in the evening session may decrease the threshold in that session. The results of the current study therefore indicate that the daytime decrease in threshold may reflect at least in part the effect of reduced exposure to the stimulus

within the evening session on the measured threshold. Moreover, the results shown in Fig. 1 demonstrate a non-monotonic dependence of between-session improvement on number of trials in the session, with improvements being largest at some intermediate number of trials. These results, obtained using the same number of trials in all 3 sessions within each experiment, point to an essential interaction between visual adaptation and learning and between adaptation and consolidation. Learning is absent in the adapted condition (Fig. 1b), is present only after a night's sleep in the semi-adapted condition (Fig. 1c) and is significantly present in the less adapted condition (Fig. 1d) only after a complete 24 h cycle.

We propose that the finding of no significant gains throughout experiment 2 (Fig. 1b) suggests that over-exposure to the stimuli may increase the measured thresholds and suppress the learning processes. This interpretation can be linked to the deterioration phenomena due to repeated exposure to the task (Mednick et al., 2002, 2005) or to the presence of adaptation (Ludwig & Skrandies, 2002; Ofen et al., 2004) or to both. However, our results further indicate that the over-exposure to the stimuli may also interfere with consolidation as even an interval of 24h was insufficient to develop performance gains. More importantly, our results show that in the semi-adapted condition sleep can counteract the effect of over-exposure on learning. Such a conclusion is consistent with the results of Mednick et al. (2002) showing that a short nap (mostly slow waves sleep) can counteract the deterioration effect and with other experimental results showing a correlation between slow waves sleep homeostasis and learning of a motor task (Huber, Felice Ghilardi, Massimini, & Tononi, 2004).

We suggest a refined account of practice and performance of texture discrimination, which explains the apparent inconsistencies in major previous studies: following exposure to a stimulus, both suppressive (adaptation) and facilitatory (learning) processes are triggered resulting in sustained effects on performance. The interaction of these two processes may determine the triggering and effectiveness of memory consolidation processes, with sleep having an important role in counteracting the suppressive effects.

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