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Sleep-Dependent Learning and Practice-Dependent Deterioration in an Orientation Discrimination Task

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Abstract

Learning new information requires practice. The degree of learning can be influenced by the amount of practice and whether subjects sleep between sessions. Over-practice, however, can lead to performance deterioration. The interaction between practice-dependent deterioration and sleep-dependent learning needs more study. We examine whether the amount of practice before sleep alters learning, and whether prior sleep protects against deterioration. Two groups (*N* = 33) were tested three times across two days on an orientation discrimination task. The High practice group was tested twice before a night of sleep and once after, at 9 a.m., 7 p.m., and 9 a.m. The Low practice group was tested once before a night of sleep and twice after, at 7 p.m., 9 a.m., and 7 p.m. Overall, both groups showed (1) deterioration with repeated, within-day testing, (2) performance improvement only after a night of sleep, (3) similar amounts of sleep-dependent learning and practice-dependent deterioration. In summary, we found that sleep resets visual contrast thresholds to a lower baseline (i.e., produces learning), but does not prevent over-practice deterioration effects. Likewise, over-practice deterioration does not influence the magnitude of overnight learning on this task.

Keywords

sleep; learning; deterioration; vision; crowding

> "Man's mind, once stretched by a new idea, never regains its original dimensions."
> Oliver Wendell Holmes *US author & physician* (*1809– 1894*)

Training across multiple sessions on a visual perception task usually leads to a net improvement in performance. Improvement can occur over a period of minutes (Fahle, Edelman, & Poggio,

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1995). Larger improvements, however, are slow and may require intersession sleep episodes of either nocturnal sleep (Karni, Tanne, Rubenstein, Askenasy, & Sagi, 1994) or a nap (S. Mednick, Nakayama, & Stickgold, 2003). In humans, these improvements are accompanied by changes in blood flow to brain areas associated with processing task information (Schwartz, 2002; Walker, Stickgold, Alsop, Gaab, & Schlaug, 2005) and alterations in local field potentials (Shoji & Skrandies, 2006; Skrandies & Fahle, 1994). In animals, learning has been correlated with changes in tuning functions (Schoups, Vogels, Qian, & Orban, 2001) in V1, (Raiguel, Vogels, Mysore, & Orban, 2006) in V4, and coordination of oscillatory activity across brain structures associated with learning and memory (Decoteau et al., 2007). In a meta-analysis of perceptual learning studies, Fine and Jacobs (2002) reported that the rate of perceptual learning is modulated by the complexity of the stimulus (i.e., simple targets presented alone showed smaller learning rates than targets with distractors).

Training, however, does not always lead to improvement. Recent studies show that repeated same-day testing produces decreases in performance (i.e., deterioration) (S. Mednick et al., 2003; S. C. Mednick et al., 2002). Deterioration has been associated with the amount of training and specific features of the target (S.C. Mednick, Arman, & Boynton, 2005). However, the cause of deterioration is unclear. One hypothesis suggests that the integrity of the memory representation may be vulnerable to practice-induced deterioration. Indeed, studies have shown that memories are not stable across time and their trace may be mutable at every stage of consolidation (Nader, Schafe, & LeDoux, 2000; Walker, Brakefield, Hobson, & Stickgold, 2003). In addition, the presentation of a secondary task before sleep can block consolidation of the primary task (for review see Stickgold & Walker, 2005). It is unknown, however, whether repeated testing of the same task, which produces deterioration, will attenuate consolidation in the same way as a secondary task. If so, then the degree of deterioration should be inversely correlated with the amount of postsleep improvement, because greater deterioration would lead to a weaker memory trace to be consolidated during sleep. Censor and colleagues addressed this question with a more complex texture discrimination task and showed that increasing the number of within session trials can eliminate subsequent learning from sleep (Censor, Karni, & Sagi, 2006). Although Censor's data may be correct, their sample of five subjects is too small to discriminate group differences in perceptual learning studies. Furthermore, we can ask whether a memory consolidated by sleep is still vulnerable to practice-dependent deterioration. No studies have examined the interaction between these practice-effects (facilitation and deterioration) and the sleep-dependent enhancement period. Here, our primary focus is to examine this question by manipulating practice load before sleep and measuring its effect on postsleep performance.

We examined whether learning and deterioration effects would be modulated by the presence of distractors. In our orientation discrimination task, a Gabor stimulus was either presented alone or surrounded by four flankers, each made up of both target orientations superimposed (forming a “plaid”). We examined three questions. (1) Does perceptual deterioration negatively impact subsequent sleep-dependent perceptual learning? (2) Does sleep-dependent learning prevent subsequent perceptual deterioration? (3) Does the presence of distractors modulate the magnitude of perceptual learning and deterioration?

Method

Participants and Procedures

A total of 33 participants gave informed consent to participate in the study, which was approved by the internal review board of the Salk Institute for Biological Studies. All participants, ages 18 through 40, had normal or corrected-to-normal vision. Participants were restricted from caffeine the day of the study, restricted from alcohol the evening before test day, and were asked to get at least 7 hours of sleep on both the night before the study, and the experimental night.

Each participant was randomly assigned to one of two groups: Low practice (*n* = 16) or High practice (*n* = 17). Low practice subjects were tested only once before the overnight sleep episode, whereas High practice subjects were tested twice before sleep. The Low practice group tested at 7 p.m. Day 1 and again at 9 a.m. and 7 p.m. Day 2, and the High practice group was tested at 9 p.m. and 7 p.m. Day 1 and again at 9 a.m. Day 2. The major difference between these two groups was the amount of practice with the task before a night of sleep. Figure 1 illustrates the timeline for the study.

Each session lasted 60 to 75 minutes. Participants were tested in a dimly lit quiet room. The participants' heads were stabilized using a chin rest, maintaining a distance of 57.5 cm from the computer screen. The stimuli were programmed in Matlab and PsychToolbox (Pelli, 1997) and presented using a PC and a Sony CRT computer monitor. The monitor's luminance was measured using a Tektronix J18 Lumacolor II photometer with a J1800 series sensor head and an online luminance calibration was applied to all stimuli.

Task

Subjects were required to discriminate a peripheral target consisting of a Gabor oriented either at 45 degrees or 315 degrees. The target was 8.5 degrees from fixation (6 degrees to the side, and 6 degrees up and 3 degrees in diameter; the flankers were the same size and had a center-to-center separation from the target of 3 degrees). Spatial frequency was 2 cycles/degree and the Gaussian window had a standard deviation of .5 degrees. We tested two stimulus configurations. In the Crowded condition, four surrounding distractors flanked the target, and in the Uncrowded condition, the target was presented alone in the visual field. Targets appeared for 32 ms, followed by an inter-stimulus-interval and then a mask. Distractors and mask stimuli were composed of 45 degrees and 135 degrees Gabors additively superimposed on one another (to create a plaid). Target contrast decreased with correct discrimination responses. Performance was measured as the target contrast that led to 75% correct in a staircase procedure. The staircase decreased target contrast by 10% per correct response and increased target contrast by 30% per incorrect response. Examples of task stimuli are illustrated in Figure 2.

The training procedure, which preceded session one, consisted of verbally explaining the task procedures and showing examples of the Crowded and Uncrowded target displays. Subjects then performed two blocks of 80 trials each, which served as training. Pilot studies indicated a strong effect of crowding on target-to-mask inter-stimulus-intervals (ISI); therefore, we used the training session to acquire a rough estimate of the ISI in each condition for each subject. Four ISIs were tested during training for each condition (Crowded Condition ISI in millisecond: 149, 183, 216, 249; Uncrowded condition: 17, 50, 83, 116) to determine the ISI that produced a performance level of 80% correct. Stimulus parameters were the same for the training and the actual experiment, with target contrast beginning at 100%, flanker contrast maintained at 75% and mask contrast maintained at 100%. At the start of the first test session, we settled on ISIs that yielded approximately 80% correct performance during initial training. The experiment followed with the ISIs kept constant across all three sessions at the timing determined during training. Each session contained 18 blocks, 64 trials per block with both Crowded and Uncrowded trials randomly intermixed. Our performance pattern shows that the rough approximation of 80% correct with a particular ISI left substantial fine tuning in target contrast before subjects reached their "true" 75% correct threshold. For the present study, the threshold of interest was the average of the final five blocks each session (although the reported results are robust to small changes in the number of blocks used to compute mean thresholds).

Analyses

We tested the effect of Crowding with a paired-samples *t* test for ISI presented in Crowded and Uncrowded conditions. To ensure the groups did not start out with different levels of performance because of differences in the time of day for baseline (i.e., session one) testing, we tested baseline thresholds between both conditions with a paired-samples *t* test. We examined overall effects using an analysis of variance (ANOVA) with one between subjects' variable: Group (Low vs. High practice), and two within subject variables: Crowded (Crowded and Uncrowded) and Time (session number).

We addressed the general question of whether practice lead to significant differences on contrast discrimination thresholds in the Group × Time interaction, collapsing across Crowding conditions. We address the more specific questions of (1) whether perceptual deterioration negatively impacted subsequent sleep-dependent perceptual learning and (2) whether sleep-dependent learning prevents subsequent perceptual deterioration practice effects by creating difference scores representing an Overnight difference score in both groups (session one-two and session two-three in the Low Practice and High Practice groups, respectively) and a Within-day difference score for both groups (session two-three and session one-two in the Low Practice and High Practice groups, respectively). We then used ANOVAs to examine the main effect of Group on Overnight difference score and Within-day difference score changes (ANOVAs were used rather than *t* tests to control for multiple comparisons).

We also examined the effect of Crowding on learning and deterioration in a parallel manner by collapsing across Group (i.e., level of practice). That is, we derived an Overnight difference score and a Within-day difference score for the Crowded and Uncrowded conditions. Finally, we also ran a separate Group × Time ANOVA for each Crowding condition and used post hoc pairwise comparisons to assess differences between each pair of training sessions.

Results

Average threshold ISIs were 208 and 96 ms for Crowded and Uncrowded conditions, respectively, demonstrating that the presence of distractors significantly increased the threshold ISI in the Crowded condition compared with the Uncrowded condition, $t(34) = 13.41$, $p < .0001$, partial eta^2 = .91. This large difference in the ISI confirms that the distracters did significantly interfere with target processing. Furthermore, baseline contrast discrimination thresholds at session one were not significantly different ($F(1, 31) = .58$, $p = .45$, partial eta^2 = .02), suggesting that the ISI manipulation succeeded in equating the difficulty of the Crowded and Uncrowded displays. Figure 3 shows the overall performance as the within-session averaged thresholds across 18 blocks for both the High Practice and Low Practice groups.

We next examined the effects of practice on contrast discrimination thresholds, and found a significant Group × Time interaction ($F(2, 30) = 14.0$, $p = .001$, partial eta^2 = .48), as well as a significant main effect of Time ($F(2, 30) = 3.9$, $p = .03$, partial eta^2 = .20). The effect of Group on the Overnight difference score was not significant ($F(1, 31) = .61$, $p = .42$, partial eta^2 = .02). Thus, the amount of practice (and therefore, practice-dependent perceptual deterioration) before sleep did not interfere with sleep-dependent learning. The effects of Group on the Within-day difference score was also not significant ($F(1, 31) = .16$, $p = .60$, partial eta^2 = .00). Thus, a prior night of sleep did not protect against within-day deterioration.

In examining whether Crowding affected sleep-dependent learning, there was a nonsignificant effect of Crowding on the Over-night difference score (.17 and .10 contrast difference for Crowded and Uncrowded conditions, respectively, $F(1, 32) = 3.21$, $p = .08$, partial eta^2 = .09). There was also a nonsignificant effect of Crowding on the Within-day difference score (.09 and .04 contrast difference for Crowded and Uncrowded conditions, respectively, $F(1, 32) =$

2.49, p = .12, partial eta^2 = .07). Although the data only support trend level effects of crowding on sleep-dependent learning and practice-dependent deterioration, close examination of the data appears to show that there may be a difference in magnitude of learning and deterioration effects between the crowding conditions (Figures 4 and 5). To investigate this more closely, we performed a post hoc analysis examining the Group × Time interaction for each crowding condition separately.

For the Crowded Condition (see Figure 4), the Group × Time interaction was significant (F(2, 30) = 14.96, p = .001, partial eta^2 = .49), as was the main effect of Time (F(2, 30) = 4.20, p = .03, partial eta^2 = .11). The main effect of Group was not significant (F(1, 31) = 2.42, p = .1, partial eta^2 = .07). Looking at the specific interaction contrasts, sleep-dependent learning in both the Low practice group (session one to session two), t(15) = 3.04, p = .008, partial eta^2 = .38, and the High practice group (sessions two to three) was significant, t(16) = 4.01, p = .001, partial eta^2 = .63. Within-day deterioration was also significant in both groups [Low practice sessions two to three: t(15) = −2.99, p = .009, partial eta^2 = .36; High practice sessions one to two: t(16) = 2.63, p = .02, partial eta^2 = .25]. Thus, similar to the general findings above, there were no differences in the overnight learning between the High and Low practice groups (.15 vs. .13 contrast change, Low vs. High practice group, t(31) = .31, p = .75) and small but nonsignificant differences in within-day deterioration between groups (−.06 vs. −.10 contrast change, Low vs. High practice group, t(31) = .55, p = .12).

In the Uncrowded condition (see Figure 5), the Group by Time interaction was significant (F(2, 30) = 4.0, p = .03, partial eta^2 = .21), but neither the main effect of Group (F(1, 31) = .52, p = .47, partial eta^2 = .01), nor the main effect of Time (F(2, 30) = 2.72, p = .07, partial eta^2 = .08) were significant. Looking at the specific interaction contrasts, sleep-dependent learning in the Low practice group was not significant (sessions one to two), t(15) = 1.23, p = .24, partial eta^2 = .06, whereas the High practice group showed significant overnight improvement (sessions two to three), t(16) = 3.35, p = .004, partial eta^2 = .44. Within-day deterioration was not significant in either group (Low practice: t(15) = −.77, p = .46, partial eta^2 = .02; High practice: t(16) = −1.63, p = .12, partial eta^2 = .10).

Conclusions

We examined the relationship between practice-dependent perceptual deterioration and sleep-dependent perceptual learning in both Crowded and Uncrowded visual conditions. Similar to previous findings (Censor et al., 2006; S.C. Mednick et al., 2005, 2002), we show that increasing the amount of practice on an orientation discrimination task leads to performance deterioration. However, the High and Low practice groups showed the same level of improvement after a night of sleep, even though the high-practice group showed significant performance decreases before sleep. Therefore, practice-related deterioration did not interfere with sleep-related improvements, suggesting that the memory trace upon which sleep presumably acts was not deteriorated. Likewise, both groups showed equivalent within-day deterioration, despite the fact that the Low practice group had overnight sleep after initial training. It appears then, that sleep can reset the baseline threshold (i.e., improve performance), but does not protect against further performance deterioration. Overall, the amount of postsleep improvement and postpractice deterioration was the same in both the High and Low practice groups. Since practice- and sleep-effects did not appear to influence one another, we hypothesize that the mechanisms underlying learning and deterioration function independently. Consistent with this hypothesis, Mednick and colleagues examined perceptual deterioration with a more complex, texture discrimination task and found differences in specificity profiles between learning and deterioration. Both learning and deterioration were eliminated by changing the retinotopic location of the target. However, learning was specific to the background but not the target orientation (Karni & Sagi, 1993), whereas deterioration was specific to the target but not the background orientation (S.C. Mednick, Arman, & Boynton, 2005). These data suggest separate underlying mechanisms that occur within the same cortical areas.

Although the effects were small, the magnitude of perceptual learning and deterioration appeared greater in the Crowded condition compared with the Uncrowded condition. Both groups showed learning and deterioration in the Crowded conditions; however, the only significant effect in the Uncrowded condition was sleep-dependent improvement in the High Practice group. This difference in magnitude of learning and deterioration in the two Crowding conditions is represented in the effect sizes of both the Group × Time interaction and the pairwise comparisons, which are all larger in the Crowded condition. Furthermore, because Crowded and Uncrowded trials were intermixed within session, if there was any generalization of learning across conditions, we may actually be underestimating the true size of the crowding effect. Nonetheless, these data are consistent with other studies showing weaker learning effects for targets alone (Adini, Sagi, & Tsodyks, 2002; Fine & Jacobs, 2002) and stronger learning for targets with flankers (Adini et al., 2002). This is, however, the first study to investigate the interaction between suppressive flankers that cause crowding and sleep-dependent learning and deterioration. And a focused research effort will likely be required to clearly resolve this issue. In addition, circadian effects on learning and deterioration have not been properly examined in the present study. Future studies will seek to disentangle practice and sleep effects, while controlling for time of day.

Although the mechanisms underlying learning and deterioration are unknown, neural plasticity underlying perceptual learning has been hypothesized to occur through the selective reweighting of neurons (Petrov, Dosher, & Lu, 2005; Saarinen & Levi, 1995) or through the optimization of tuning functions (Raiguel et al., 2006; Schoups et al., 2001) of all related mechanisms (i.e., neurons selective to the relevant feature) (Fine & Jacobs, 2002). These practice-dependent neural changes appear to be context-dependent (Crist, Kapadia, Westheimer, & Gilbert, 1997) and may take place sequentially or via lateral mechanisms (Gilbert, Sigman, & Crist, 2001) throughout the visual system. It is therefore possible that more complex, or crowded, visual stimuli recruit larger networks of brain areas and increase the amount of facilitation and/or suppression across the entire network. These networks may require neuronal activity to a level sufficient for plasticity to occur, whereas targets alone may activate suboptimal levels of neuronal networks. Similar models have been suggested with context-induced learning mechanism mediated by changes in the relative proportions of the excitatory and inhibitory activities in the local visual circuits (Adini et al., 2002).

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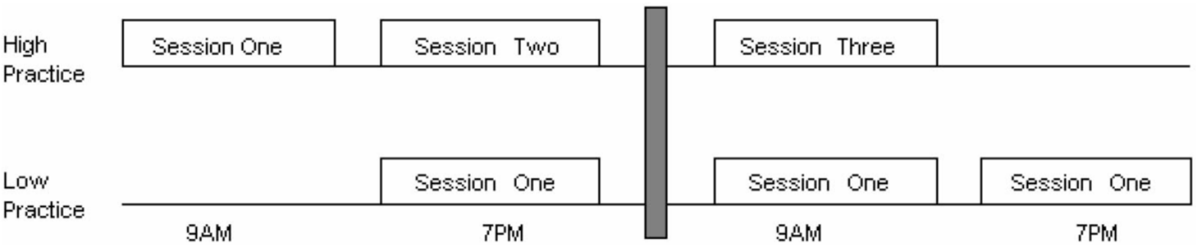

Figure 1.
Timeline for two experimental groups across 48 hours. *High practice* was tested at 9 a.m. and 7 p.m. on Day 1, and at 9 a.m. on Day 2. *Low practice* was tested at 7 p.m. on Day 1, and at 9 a.m. and 7 p.m. on Day 2. Gray bar indicates nocturnal sleep.

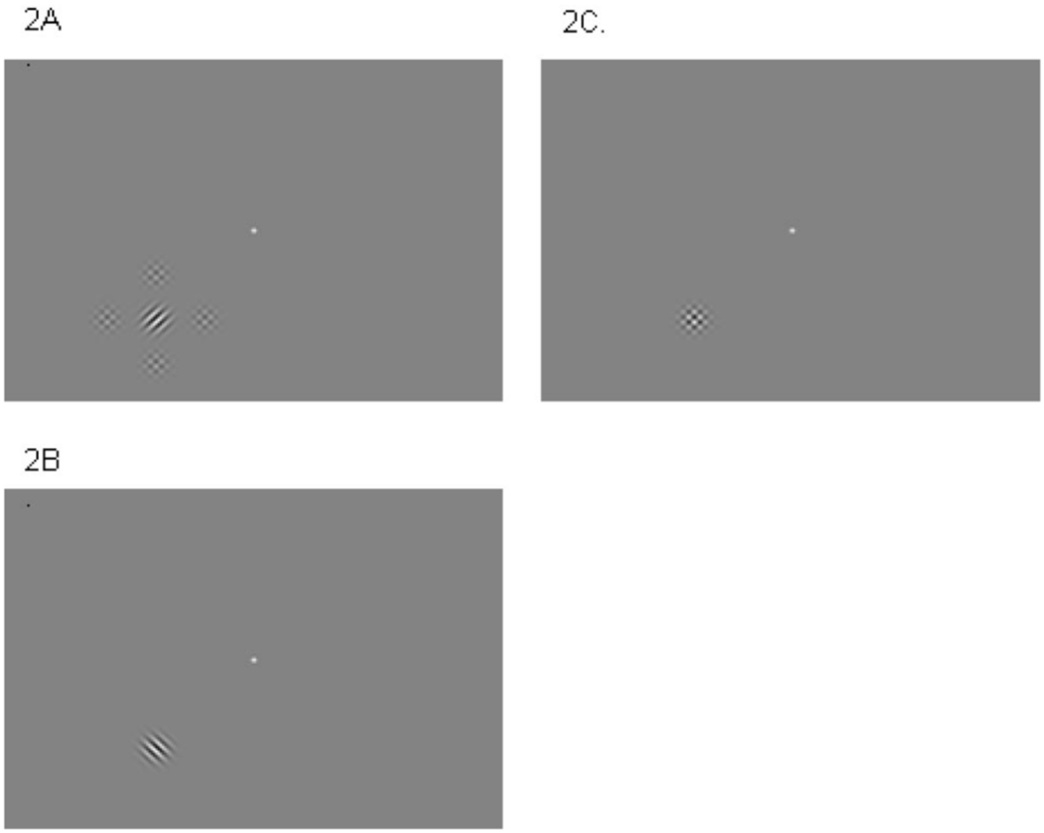

Figure 2.
Task images. Subjects focused on a fixation cross in the middle of the screen. In a lower quadrant (left in this example) the target appeared either in the Uncrowded condition (2B) or Crowded condition (2A), followed by a mask (2C).

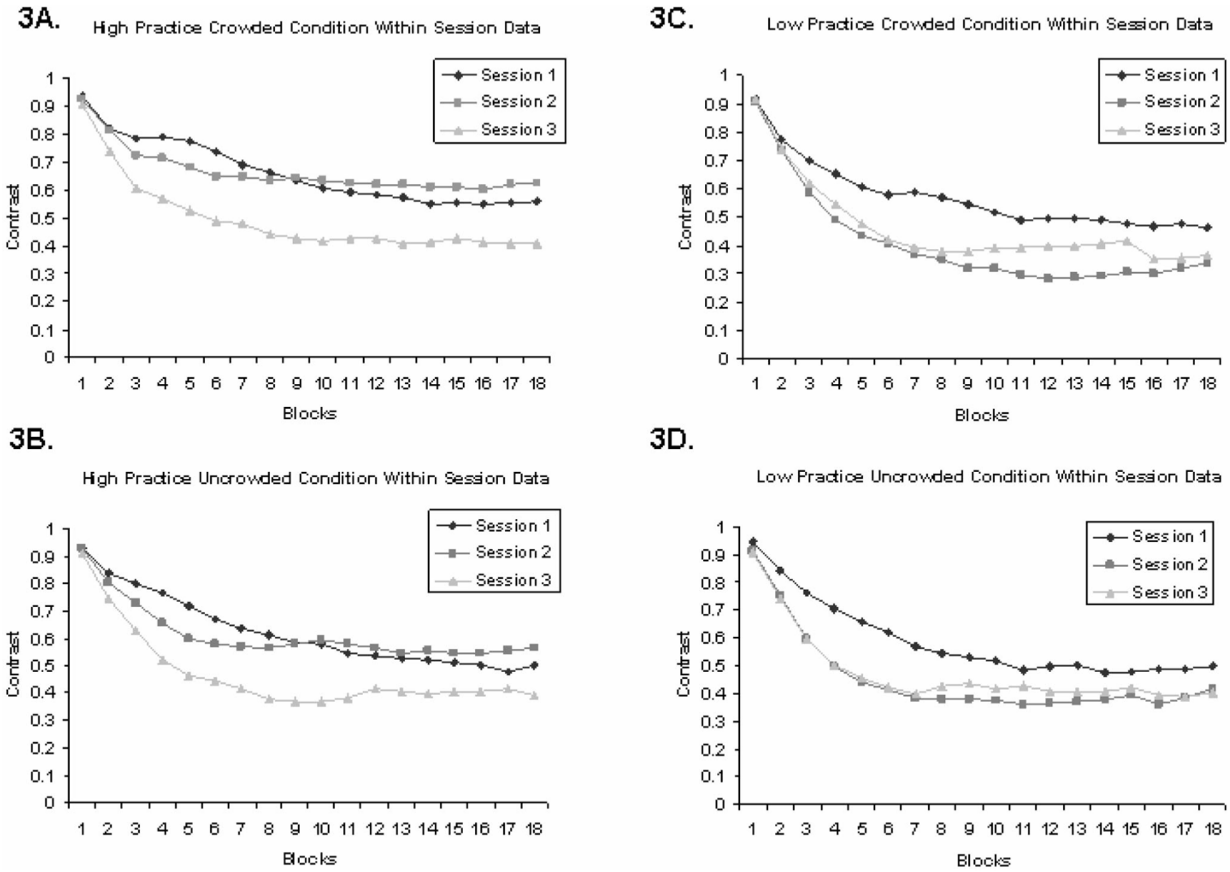

Figure 3.

Within session averages for blocks 1 through 18 for each condition presented for (3A) High Practice Crowded condition, (3B) High Practice Noncrowded condition, (3C) Low Practice Crowded condition, (3D) Low Practice Noncrowded condition.

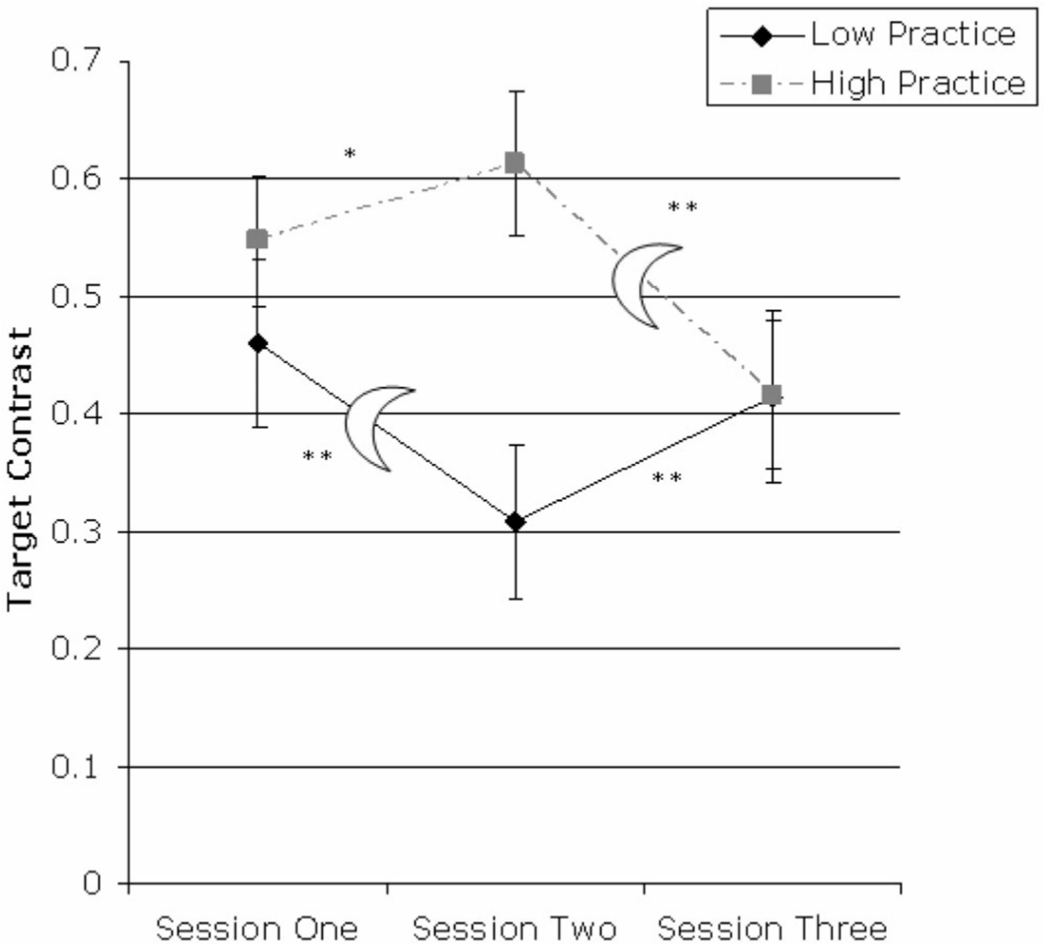

Figure 4.

Target contrast across three sessions in the Crowded condition. Half moons indicate the position of the night of sleep. Low Practice group (in black diamonds) slept between sessions one and two and showed improvement after a night of sleep ($p = .01$) and deterioration after the repeated within day session on Day 2 ($p = .01$). High Practice group (in gray squares) showed deterioration after repeated within day session on Day 1 ($p = .05$) and learning after a night of sleep on Day 2 ($p = .01$).

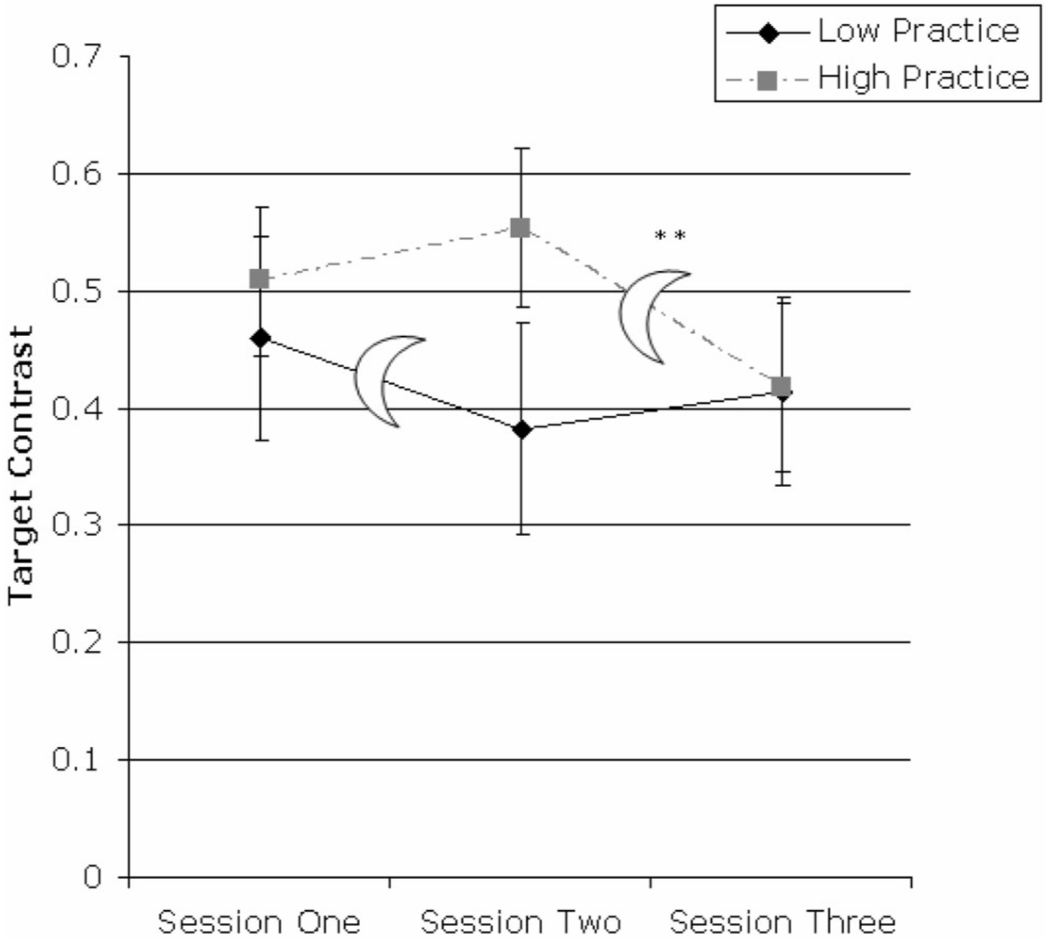

Figure 5.

Target contrast across three sessions in the Uncrowded condition. Half moons indicate the position of the night of sleep. Low Practice group (in black diamonds) slept between sessions one and two and showed no changes in contrast threshold across the three sessions. High Practice group (in gray squares) showed no changes in performance except for learning after a night of sleep on Day 2 (*p* = .01).