Visual-oculomotor interactions facilitate consolidation of perceptual learning

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Visual skill learning is commonly considered a manifestation of brain plasticity. Following encoding, consolidation of the skill may result in between-session performance gains. A great volume of studies have demonstrated that during the offline consolidation interval, the skill is susceptible to external inputs that modify the preformed representation of the memory, affecting future performance. However, while basic visual perceptual learning is thought to be mediated by sensory brain regions or their higher-order readout pathways, the possibility of visual-oculomotor interactions affecting the consolidation interval and reshaping visual learning remains uncharted. Motivated by findings mapping connections between oculomotor behavior and visual performance, we examined whether visual consolidation can be facilitated by visual-oculomotor interactions. To this aim, we paired reactivation of an oculomotor memory with consolidation of a typical visual texture discrimination task. Importantly, the oculomotor memory was encoded by learning of the pure motor component of the movement, removing visual cues. When brief reactivation of the oculomotor memory preceded the visual task, visual gains were substantially enhanced compared with those achieved by visual practice per se and were strongly related to the magnitude of oculomotor gains, suggesting that the brain utilizes oculomotor memory to enhance basic visual perception.

Introduction

Visual perception can improve with practice, adapting human behavior to the surrounding environment (Karni & Sagi, 1991; Sagi, 2011; Sasaki, Nanez, & Watanabe, 2010). In the adult brain, visual skill learning processes that yield persistent performance increments have been associated with large-scale networks, ranging from early visual processing pathways to high-order readout and feedback regions (Sagi, 2011; Shibata, Sagi, & Watanabe, 2014). Following learning termination, a cascade of neural events is initiated, resulting in reorganization of brain regions that consolidate the learnt skill into a new memory trace (Censor, Sagi, & Cohen, 2012; Dudai, Karni, & Born, 2015; Lechner, Squire, & Byrne, 1999; Wymbs, Bastian, & Celnik, 2016). In the visual domain, improved performance, that was not obtained during the initial practice session, might be evident when the skill memory is retrieved, implying offline learning mechanisms (Amar-Halpert, Laor-Maayany, Nemni, Rosenblatt, & Censor, 2017; Karni & Sagi, 1993). Moreover, studies showed that competing visual stimuli or noninvasive brain stimulation following training may interfere with consolidation, degrading future visual performance (De Weerd et al., 2012; Yotsumoto, Chang, Watanabe, & Sasaki, 2009). The notion that memories are labile to modifications during offline processes raises the possibility for memory interactions, as recently shown between motor and declarative skills (Mosha & Robertson, 2016). However, whether visual consolidation processes enable such flexible visual-oculomotor modulations is unknown.

Based on evidence regarding interactions between motor preparation of hand (Rolfs, Lawrence, & Carrasco, 2013) or eye (Li, Barbot, & Carrasco, 2016; Rolfs, Murray-Smith, & Carrasco, 2018) movements and visual perception, here we investigated whether an oculomotor skill can facilitate visual skill consolidation. To this aim, we sought to create an interaction between an already consolidated oculomotor memory trace with the consolidation of a visual task. To enable such interactions, we developed an experimental design.
pairing reactivation of an oculomotor memory with visual learning (Figure 1). This was achieved by using the framework of memory reactivation, according to which reactivation of a consolidated memory evokes consolidation-like processes that allow neural plasticity mechanisms to stabilize and update learning and memory (Amar-Halpert et al., 2017; Bang et al., 2018; Nader & Hardt, 2009). On the first day, subjects in the visual + oculomotor reactivation group learned to execute eye movements to a specific retinotopic location while the fixation starting point was randomly varied, to create an oculomotor memory (see Figure 1A and the Materials and Methods section). Importantly, the oculomotor memory was encoded by learning of the pure motor component of the movement, removing visual cues. The oculomotor memory was reactivated on the consecutive day with a short reminder, prior to an encoding session of a standard visual texture discrimination task (TDT; Karni & Sagi, 1991; see Figure 1B and the Materials and Methods section). In the TDT, the target occupied the same retinotopic location that was used in the oculomotor task (see the
Materials and Methods section). We therefore hypothesized that oculomotor memory reactivation paired with visual learning would enable the neural networks of both tasks to interact. The use of similar retinotopic coordinates was based on previous studies suggesting that online interactions between movement intention and visual performance were spatially dependent (Rolfs et al., 2013; Schneider, Einhauser, & Horstmann, 2013). On the third day, subjects were retested on the visual discrimination task and then on the oculomotor task. We hypothesized that the oculomotor reactivation would result in enhanced between-sessions visual learning gains (Karni & Sagi, 1993). To test whether oculomotor reactivation enhanced visual learning, we compared the visual gains achieved by pairing the oculomotor memory reactivation and the visual learning (i.e., the reactivation group) to those obtained by a standard learning procedure in which subjects (visual group, measured in a previous study; Amar-Halpert et al., 2017) performed the visual task on 2 consecutive days.

Materials and methods

Subjects

Eighty-six naive healthy subjects, ages 18 to 40 years (60 female, average age 24.0 years, SD = 3.5 years) gave their written informed consent to participate in the experiments, which were approved by the Tel Aviv University Institutional Ethics Committee. All procedures were in accordance with approved guidelines. All participants had normal or corrected-to-normal vision, were not video gamers, did not participate in other visual experiments during the current experiment period, and reported at least 6 hours of sleep the night before each experimental session.

Two subjects were excluded from the study because of repeated mistyping errors already in the first session, which prevented reliable measurement of the peripheral discrimination threshold. Data from six subjects were not included only in the oculomotor analysis (three in the oculomotor reactivation group, one in the oculomotor no-reactivation group, two in the oculomotor exposure group) because of corrupted or incomplete (less than 10 out of 32 trials) eye-movement data files.

Stimuli and tasks

Oculomotor task

Each trial started with a black fixation point (diameter 1°) appearing on a random location on the screen (CRT HP p1230 monitor, refresh rate 100 Hz). Locations were uniformly distributed across screen quadrants and randomly distributed within each quadrant. A head rest was used, and subjects maintained fixation for 1 s (controlled by monitoring gaze position). After the fixation disappeared, subjects were required to execute an eye movement toward a target location (diameter 1°) that was always at the same distance (5.71° visual angle, same retinotopic coordinates as in the visual task) and angle (–45°) from the starting fixation. No a priori visual cues marked the target location, to abolish visual information that could guide the movement. Instead, auditory feedback was given for errors. This, together with the random locations of the saccade’s target (relative to the randomly appearing starting fixation), ensured that the saccade’s target location could not be predicted by any visual information. On Day 1, subjects completed one pretraining block, followed by four training blocks and a test block, with 32 trials each (a total of 192 trials). Prior to the pretraining block, a static screen with an example fixation and a black circle that marked the target location was presented to the subjects, while the experiment’s instructions were delivered. Following the pretraining block, subjects completed a feedback block, in which each trial ended with a visual feedback screen, presenting the saccade landing point (with a red dot), the starting fixation, and a black circle that marked the target location. Importantly, the feedback screen appeared immediately after the movement terminated and the eyes landed on a new location; thus, the movement was independent of visual cues. Then, three training blocks were conducted, each starting with four feedback trials, followed by the 32 regular trials without feedback (see above). In between every set of eight regular trials, a static example screen appeared, and subjects pressed the space bar to continue. Finally, subjects completed a test block that was identical to the pretraining block.

Texture discrimination task

Participants performed a standard TDT (Karni & Sagi, 1991), with a target frame (10 ms) followed by a patterned mask (100 ms; Figure 1B). They were asked to discriminate whether a target stimulus consisting of three diagonal bars (presented at the lower right quadrant of the visual field at 5.71°) was horizontal or vertical. The target was embedded in a background of horizontal bars (19 × 19, 0.58° × 0.04° each, spaced 0.82° apart with 0.04° jitter). Fixation was enforced by a forced-choice letter discrimination task (“L” or “T” at the center of the display) with auditory feedback for errors. Display size was 15.6° × 15.1° (viewed from 97 cm away on a 20-inch CRT HP p1230 monitor, refresh rate 100 Hz, mean texture luminance 84 cd/m²). The intervals between the target and the mask stimuli
(stimulus onset asynchrony [SOA], measured from the onset of the target to the onset of the mask) ranged from 40 to 340 ms (40, 60, 80, 100, 120, 140, 160, 180, 200, 220, 240, 260, 300, and 340 ms) and were randomized across all trials. Each block consisted of 18 trials per SOA (for a total of 252 trials over nine blocks). To familiarize the subjects with the task, pretraining blocks of 10 trials at 500 ms and then at 340 ms SOA were repeated until subjects reached 90% correct responses (a maximum of 10 blocks, after which subjects who did not reach the criterion did not participate in the experiment). Pretraining blocks were followed by a short familiarization block of a single trial per each SOA.

**Experimental design**

In the first experiment, we tested whether oculomotor memory can enhance between-days visual perceptual gains, compared with visual gains obtained following standard practice. On the first day (Day 1), participants in the oculomotor reactivation group (n = 18) learned the oculomotor task. On the consecutive day (Day 2), participants reactivated the oculomotor memory by performing 10 trials of the oculomotor task. Immediately following the oculomotor reactivation, participants completed a full session of the visual TDT. On the following day (Day 3), subjects were retested on the TDT again, followed by a retest block of the oculomotor task (Figure 1C). Retest blocks were identical to the test blocks in each task. Subjects in the visual group (n = 12) performed the standard test-retest of the TDT on 2 consecutive days, without the oculomotor task.

In the second experiment, we tested whether the visual gains could be facilitated without oculomotor task. One subject in that group performed repeated mistyping errors in the final session, which prevented reliable measurement of the peripheral discrimination threshold. This subject was therefore retested again on the following day to achieve a reliable learning gain assessment.

**Data analysis**

**Oculomotor task data analysis**

Binocular eye movements were monitored using a remote infrared video-oculographic system (Eye-link1000 Plus; SR Research Ltd., Ontario, Canada), with spatial resolution of 0.01° and averaged accuracy of 0.25° to 0.50° visual angle, sampled at 1,000 Hz. A nine-point calibration procedure was performed at the beginning of each session and repeated when the subject’s starting fixation was not detected.

Throughout the experiment, a gaze-contingent procedure was used to monitor eye movements in real time. Onsets of eye movements were detected based on a sliding window of 150 samples, with a radius of 1° visual angle around the average gaze position. Movement was detected when at least one sample was outside the defined area, in at least one eye. This algorithm yielded comparable results to the offline movement detection algorithm (95%, see below).

Gaze contingency was used to provide auditory feedback for incorrect responses, which were excluded when distance larger than 1° from the center of the target location. Gaze contingency was also used to alert participants by a warning text if they shifted their gaze when not required (“fixation-break”) or when they did not execute a saccade after a fixation offset (“no movement was detected”). The gaze contingency algorithm was also able to control for blinks as fixation breaks. Trials in which fixation was broken or no movement was detected were aborted, discarded from analysis, and repeated at the end of the block, to maintain equal probability of the trial conditions.

Saccades were detected offline using a published algorithm (Engbert & Kliegl, 2003) and analyzed using MATLAB (MathWorks, Natick, MA). An elliptic threshold criterion for saccades detection was determined in two-dimensional velocity space, based on the horizontal and vertical velocities of the eye movement. Specifically, the threshold was set to be six times the SD of the eye movement velocity, using a median-based estimate of the SD. Additional parameters used for saccade detection were the following: minimal amplitude threshold of 1° visual angle, minimal saccade duration of 6 ms, and minimal interval between saccades of 50 ms. Fixations were defined as the time intervals between the saccades.
ments and removed from the analysis. In addition, trials in which the onset of the movement was not reliably detected (preceding fixation disappearance by more than 150 ms) or in which the saccade’s velocity and amplitude could not be detected were considered invalid trials and were removed from the analyses. The average number of valid trials for each subject was 27.7 per block (out of 32).

Texture discrimination task data analysis

The perceptual threshold was measured for each session using a standard Weibull fit for a psychometric curve, with slope $\beta$ and finger error (mistyping) parameter $1 - p$, yielding the function (Censor, Karni, & Sagi, 2006):

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

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

where $T$ is the threshold for each curve, defined as the SOA for which $81.6\%$ of responses were correct.

Statistical analysis

Oculomotor performance was measured as saccade error (distance from the target location). Repeated-measures analysis of variance (ANOVA), with blocks as a factor, was calculated to assess the difference between pretraining, test, and retest blocks in both experiments. Planned comparisons were used to assess learning gains between the test and retest blocks. In the second experiment, a comparison between exposure and no-reactivation retest blocks was conducted using a two-tailed independent $t$ test, to assess whether oculomotor consolidation processes occurred following the brief exposure.

Perceptual thresholds were extracted for each day separately. Comparisons of visual learning gains were conducted using repeated-measures ANOVA with group as the between-subject factor and days as the within-subject factor. An analysis of covariance was conducted with initial thresholds as covariate. To further confirm that the results do not support the null hypothesis, a Bayesian analysis was performed (Berger & Sellke, 1987).

Results

Repeated-measures ANOVA with days as a within-subject factor and group as a between-subject factor revealed that when brief reactivation of the oculomotor memory preceded the visual task (visual + oculomotor reactivation group, $n = 18$), subsequent between-days visual learning gains (mean test-retest threshold improvements of $35.0 \pm 7.8$ ms standard error, constituting a total improvement of $22.2% \pm 4.2\%$) were substantially enhanced relative to learning achieved with visual practice per se (visual group, $n = 12$; $9.9 \pm 8.4$ ms, $2.9\% \pm 5.8\%$), with a significant day $\times$ group interaction, $F(1, 28) = 4.50, p = 0.043$ (Figure 2A). A complementary Bayesian analysis confirmed that the data do not support the null hypothesis ($BF_{01} = 0.516 \pm 0.03$). The results were maintained when initial thresholds were included as a covariate in the analysis, with a significant effect of group, $F(1, 27) = 5.66, p = 0.025$, and an insignificant interaction with the initial thresholds, $F(1, 26) < 0.01, p > 0.9$ (see the Materials and Methods section).

Oculomotor saccade error (see the Materials and Methods section) was reduced across blocks (repeated-measures ANOVA with blocks as within-subjects factor), $F(2, 28) = 13.82, p < 0.001$, revealing significant between-days learning gains (mean error reduction between days of $0.3^\circ \pm 0.1^\circ$ visual angle, $t(14) = 2.56$, $p = 0.022$, total of $15.6\% \pm 7.3\%$; Figure 2B). The magnitudes of individual visual and oculomotor learning gains were strongly related (correlation between test-retest improvements $r = 0.69$, $p = 0.004$), further supporting the notion that visual-oculomotor interactions are involved in learning facilitation (Figure 2C). There was no correlation between initial visual thresholds and oculomotor gains ($r = 0.19, p = 0.49$).

Could perceptual learning be facilitated without reactivation of the oculomotor memory or as part of a postexposure enhancement effect without sufficient consolidation of the oculomotor memory? To address these questions, we conducted an additional experiment comparing standard visual practice (visual replication group, $n = 18$) with a condition in which the oculomotor memory was not reactivated (visual + oculomotor no-reactivation group, $n = 18$; Figure 3A) and a condition in which participants were exposed to the nonconsolidated oculomotor task prior to the visual task (visual + oculomotor exposure group, $n = 18$; Figure 3B), using the same number of trials that was used to reactivate the oculomotor memory.

Visual learning gains without oculomotor reactivation (visual + oculomotor no-reactivation group, $16.5 \pm 4.8$ ms, $13.2\% \pm 3.3\%$) or following exposure to the nonconsolidated oculomotor task (visual + oculomotor exposure group, $17.9 \pm 4.3$ ms, $13.8\% \pm 3.2\%$) were greater than learning gains achieved with visual practice per se (visual replication group, $10.8 \pm 8.7$ ms, $5.9\% \pm 6.0\%$), although not significantly (i.e., no Day $\times$ Group interaction), $F(2, 51) = 0.36, p = 0.70$ (Figure 4A). A complementary Bayesian analysis provided support in favor of the null hypothesis ($BF_{01} = 5.188 \pm$
In addition, the magnitude of oculomotor learning gains in the visual + oculomotor no-reactivation group (0.5° ± 0.2° visual angle, t(16) = 3.87, p = 0.001, total of 19.8% ± 4.9%, Figure 4C) did not predict visual learning gains (r = 0.11, p = 0.67; Figure 4C). Of note, performance on the third day significantly differed between the no-reactivation and exposure groups (two-tailed independent t test, t(21.32) = 3.89, p = 0.001), confirming that, indeed, the brief oculomotor exposure was not sufficient to induce oculomotor consolidation processes that could interact with visual memory consolidation (Figure 4B). Overall, the results suggest that visual-oculomotor interactions per se may operate distinctly from reactivation processes.

Figure 2. Visual gains are enhanced by visual-oculomotor interactions. (A) Individual visual thresholds at test and at retest for both visual (red) and visual + oculomotor reactivation (yellow) groups. Average thresholds per day are marked in a black line for each group. Mean learning gains are enhanced for the reactivation group compared with the visual group. (B) Oculomotor performance, measured as the movement's accuracy (saccade error, distance from target) at pretraining, test, and retest. (C) Correlation between visual and oculomotor learning gains. Error bars are SEM.

Figure 3. Design of Experiment 2. (A) The oculomotor + no-reactivation group learned the oculomotor task on Day 1. On Day 2, participants completed a full session of the visual TDT, without reactivating the oculomotor memory (see the Materials and Methods section). On Day 3, the final performance was measured for both the visual (TDT retest) and oculomotor (oculomotor retest) tasks. (B) The oculomotor exposure group performed a brief exposure to the oculomotor task (10 trials) prior to the TDT. On the following day, final performance was measured for the visual (TDT retest) and oculomotor tasks (see the Materials and Methods section).
A confirmatory analysis verified that the visual gains exhibited in the reactivation group indeed differed significantly from the visual replication group, $F(1, 34) = 4.26, p = 0.047$. In addition, visual gains achieved by the reactivation group were larger than those achieved by the no-reactivation and exposure groups (although marginally significant), $F(1, 34) = 4.07, p = 0.052$, and $F(1, 34) = 3.64, p = 0.065$, respectively. Therefore, it would be of interest in further studies to separate the contribution of visual-oculomotor interactions per se and the role of oculomotor reactivation in enhancing visual learning.

**Discussion**

The results indicate that visual consolidation can be facilitated via visual-oculomotor interactions. Reactivation of an oculomotor memory prior to visual learning and consolidation resulted in substantial enhancement of visual gains, suggesting that oculomotor memory modulated visual consolidation. Consistently, a strong correlation was observed between the oculomotor and visual gains, suggesting that the brain utilizes the oculomotor learning increments to enhance visual gains.

Oculomotor exposure and oculomotor memory without reactivation did not significantly enhance nor correlate with visual gains. The possibility that these oculomotor procedures were not sufficient to induce oculomotor processes efficiently interacting with visual memory should be examined in future studies.

The mechanisms underlying efficient oculomotor-visual between-sessions learning interactions triggered by reactivation of a consolidated oculomotor memory remain to be charted. One such possible mechanism is spatial attention, which was shown to be involved in both types of skills. Indeed, the oculomotor system has substantial overlaps with the attention network (Corbetta et al., 1998), and attention shifts are involved in goal-directed eye movement (Corbetta & Shulman, 2002). In addition, attention has been shown to facilitate visual learning (Mukai, Bahadur, Kesavabhotla, & Ungerleider, 2011; Roelfsema, van Ooyen, & Watanabe, 2010). The results are also consistent with
“selection-for-action” and “selection-for-attention” models, suggesting that spatial attention underlies coupling between visual discrimination performance and saccade programming, implying a mechanism that prioritizes visual space and affects both motor and visual domains (Deubel & Schneider, 1996; Schneider, 1995). Therefore, the oculomotor training may have enhanced attention to the specific retinotopic location, which in turn enhanced visual learning. Accordingly, such mechanisms may operate in a bidirectional manner; thus, future studies should investigate whether visual learning can affect oculomotor consolidation, shedding more light on the mechanisms underlying cross-domain offline learning interactions.

The involvement of attention may be captured as either a priming effect or a longer-term training effect. The first possibility is less plausible because the results here (oculomotor exposure group) indicate that such immediate online mechanisms did not sufficiently enhance visual consolidation. These results are consistent with previous findings within the visual domain showing that the effects of reactivation on learning are not an epiphenomenon of primed retrieval enhancement and require offline stabilization periods (Amar-Halpert et al., 2017; Bang et al., 2018). Therefore, an attentional mechanism that could trigger long-term plasticity, such as spatial training, may be involved here. Interestingly, such an attentional mechanism may operate in the absence of visual feedback as performed here, highlighting the contribution of the motor component in the saccade memory trace (Meital, Korinth, & Karni, 2013; Opris, Barborica, & Ferrera, 2003).

Studies investigating consolidation mechanisms of oculomotor and visual skills point to distributed neural networks engaged in the formation of each memory (Albouy et al., 2008; Mukai et al., 2007; Yotsumoto, Watanabe, & Sasaki, 2008), which consist of overlapping parietal and frontal regions. These may serve as network hubs, integrating memories via consolidation-induced plasticity. Such high-order overlapping memory mechanisms were recently suggested in a study revealing transfer between motor skill and word-list memories (Mosha & Robertson, 2016). Indeed, theories of visual learning suggest the involvement of high-order mechanisms that mediate performance increments with learning (Law & Gold, 2008; Mukai et al., 2007; Shibata et al., 2014; Xiao et al., 2008). Accordingly, it remains to be determined how such mechanisms may relate to oculomotor-visual interactions and the specificity of the retinotopic overlap as used here. For example, it would be relevant to determine the relation to double-training procedures in which learning transfers across spatial locations via task-irrelevant location training (Xiao et al., 2008).

Our results may have important implications for learning and memory research as well as for clinical populations experiencing difficulties in domain-specific skill learning, who could benefit from facilitatory visual-oculomotor interactions. Thus, the ability of the brain to use oculomotor learning to enhance visual learning via memory interactions may be relevant both for enhancing learning in normal settings and for conditions involving learning impairments.

**Keywords:** perceptual learning, memory consolidation, oculomotor learning

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