Reactivation-induced memory integration prevents proactive interference in perceptual learning

Zhibang Huang [1,2,3,4], Zhimei Niu [5], and Sheng Li [1,2,3,4]

[1] School of Psychological and Cognitive Sciences, Peking University.

[2] Beijing Key Laboratory of Behavior and Mental Health, Peking University.

[3] PKU-IDG/McGovern Institute for Brain Research, Peking University.

[4] Key Laboratory of Machine Perception (Ministry of Education), Peking University.

[5] Department of Psychology, University of Texas in Austin.

Correspondence concerning this article should be addressed to Sheng Li, School of Psychological and Cognitive Sciences, Peking University, 5 Yiheyuan Road, Haidian, Beijing, 10087, China. E-mail: sli@pku.edu.cn

Declaration of Interests: The authors declare no competing financial interests

Acknowledgments: This work was supported by grants from Science and Technology Innovation 2030 - Brain Science and Brain-Inspired Intelligence Project (2021ZD0200204).

Abstract

We acquire perceptual skills through training to adapt ourself to the changing environment. Accomplishing an effective skill acquisition is a main purpose of perceptual learning research. However, different perceptual trainings may interfere with each other, and thus limit the application of perceptual learning outside of laboratories. Here, we trained human participants on an orientation discrimination task. We observed a proactive interference effect that the first training blocked the second training at its untrained location. This was a more pronounced effect than the well-known location specificity in perceptual learning. We introduced a short reactivation of the first training before the second training and successfully eliminated the proactive interference when the second training was inside the reconsolidation time window of the reactivated first training. Interestingly, we found that practicing an irrelevant task at the location of the second training immediately after the reactivation of the first training could also restore the effect of the second training but in a smaller magnitude, even if the second training was conducted outside of the reconsolidation window. These results demonstrated that reactivation could facilitate the integration of multiple perceptual trainings at two levels, depending on the activated representations during the reconsolidation process. It can integrate previously trained and untrained locations to release the training-induced attentional suppression or the different trainings at these locations to facilitate the generalization of training effects between them. The findings provide us with new insight into the roles of long-term memory mechanisms in perceptual learning.

Introduction

Early theories of visual perceptual learning considered the improvement of visual functions through experience as a result of perceptual plasticity (Hochstein & Ahissar, 2002; Sagi & Tanne, 1994). A hallmark of perceptual learning that supported this proposal was the initially observed location, feature, or eye specificity of the learning effects (Ahissar & Hochstein, 1997; Ball & Sekuler, 1987; Crist et al., 1997; Fahle, 1997; Karni & Sagi, 1991; Shiu & Pashler, 1992). However, the accumulating evidence revealed by succeeding investigations pointed out that the underlying mechanism of perceptual learning is not purely perceptual. These studies have found that the learning specificity could also be explained by higher level factors such as restricted attentional processing (Donovan & Carrasco, 2018; Donovan et al., 2015; Xiao et al., 2008; Xiong et al., 2016) and modified reading-out of sensory information from decision areas (Dosher & Lu, 1998; Jia et al., 2018; Jia et al., 2020; Law & Gold, 2008). Not beyond our expectation, the roles of mnemonic processing in perceptual learning are drawing increasing attention as well. Recent investigations have suggested that perceptual learning effect is associated with the changed representation of visual stimuli in short-term memory (Jia et al., 2021) and refined consolidation process of long-term memory (Bang et al., 2018; Tamaki et al., 2020; Yang et al., 2022).

One of the ultimate goals of perceptual learning research is to promote its application in real-world (Deveau et al., 2014; Johnston et al., 2020; Sha et al., 2020). That would require the evidence of performance improvement in the contexts that are not identical to the one in the training. Intuitively, this could be achieved by facilitating the generalization of the learning effect (Harris et al., 2012; Kattner et al., 2017). However, the widely observed learning

specificity in perceptual learning was an obvious barrier against this idea. To address this issue, several procedures based on double training (Wang et al., 2014; Xiao et al., 2008), attentional cueing (Donovan & Carrasco, 2018; Donovan et al., 2015), or concept-related categories (Tan et al., 2019; Wang et al., 2016) have been proposed to improve the transfer of learning effect to untrained stimuli or retinal locations. These approaches, though successful in demonstrating the generalized learning effect, required other manipulations in addition to the trained task.

In practice, we might train the individuals on related but no identical tasks to fulfill the requirements of various applications. However, interference is a ubiquitous phenomenon when multiple learnings take place (Anderson, 2003; Herszage & Censor, 2018; Postman & Underwood, 1973) and perceptual learning was not an exception (Bang et al., 2018; Been et al., 2011; Huang et al., 2022; Seitzt et al., 2005; Shibata et al., 2017; Yotsumoto et al., 2009). It has long been suggested that the consolidation of learning-related memory traces is not a static process. Reactivating a consolidated memory can transfer it to an unstable state in which the memory can be modified and reconsolidated (Dudai, 2006; Elsey et al., 2018; Lee et al., 2017; Nader & Hardt, 2009). The cycle of reactivation and reconsolidation could occur more than once and constitutes a crucial part of the learning flexibility in daily experience.

Interestingly, recent studies have shown that reactivation could facilitate motor learning (Herszage & Censor, 2017), reward learning (Huang & Li, 2022), and perceptual learning (Amar-Halpert et al., 2017; Klorfeld-Auslender et al., 2022; but see Chen & de Beeck (2021) for learning of complex objects). Furthermore, it was proposed that reactivation-induced integration of overlapping memory traces could facilitate the generalization of learning (Morton et al., 2017; Ritvo et al., 2019; Schlichting & Frankland, 2017) and thus potentially

prevents the interference between multiple learnings (Huang & Li, 2022). Therefore, we designed a set of five psychophysical experiments to examine the role of memory reactivation and its induced memory integration in solving the potential interference between two perceptual learnings.

Methods

Participants

We totally recruited 80 participants with 16 participants from Peking University for each experiment (Experiment 1: 12 females, mean age = 19.50 years; Experiment 2: 11 females, mean age = 19.50 years; Experiment 3: 7 females, mean age = 19.69 years; Experiment 4: 11 females, mean age = 19.13 years; Experiment 5: 12 females, mean age = 19.75 years). Participants were with normal or corrected-to-normal vision and had no known neurological or visual disorders and provided written informed consent prior to the experiment. The local ethics committee approved the study.

Stimuli

Stimuli were generated in MATLAB (MathWorks, Natick, MA, USA) using Psychtoolbox 3 package (Brainard, 1997; Pelli, 1997) and presented on a dark-gray background (~36 cd/m2) on a 20-inch CRT monitor (resolution of 1024 × 768 pixels and 60 Hz refresh rate). Gamma correction was applied to the monitor. Gabor stimuli (spatial frequency = 1.5 cycle/degree, contrast = 0.8, radius = 4°) were positioned in either upper-left or lower-right visual field with an eccentricity of 6.5°. The experiment was conducted in a dimly lit room. A

chinrest was used to stabilize the head and maintain an 85 cm viewing distance.

Procedure

The present study consisted of five psychophysical experiments (Figure 1A). All experiments were completed within nine days that consisted of a pre-test session (day 1), first training sessions (days 2-6), a mid-test session (day 7), and a post-test session (day 9). The experiments differed from each other in day 8.

Orientation discrimination task. As shown in Figure 1B, each trial of the orientation discrimination task began with a 1000 ms fixation interval, followed by the presentation of the reference Gabor stimulus (155° or 55° with a uniformly distributed jitter ±3°) for 200 ms at periphery (upper-left or lower-right). After another fixation interval of 600 ms, the test Gabor stimulus was shown for 200 ms at the same location as the reference. The participants were instructed to judge whether the test stimulus was tilted clockwise or counter-clockwise relative to the reference stimulus with a keyboard within 1500 ms from the offset of the test stimulus. The orientation difference between reference and test stimuli was controlled by a three-down one-up staircase method (step size = 0.5°). This method converged to 79.4% correct responses. For the first block of each condition, the initial orientation difference was 5°. The stopping criterion of a block was 15 reversals or 100 trials, whichever was met first. The threshold in each block was determined by the mean orientation difference of the last eight reversals. The initial orientation difference of the subsequent blocks was set to be the threshold of the last block of the same condition.

Test sessions. In each test session, participants completed three runs of the orientation discrimination task. Each run consisted four stimulus conditions with one block for each

condition. The four conditions were Loc1–Ori1, Loc1–Ori2, Loc2–Ori1, and Loc2–Ori2 (Loc1 was the location for the first training, Loc2 was the location for the second training, Ori1 was the stimulus orientation for both trainings). The order of the four conditions in each run was randomized. There was no feedback during the test sessions. There was a practice of 120 trials before the pre-test session, with 30 trials for each condition. Auditory feedback was provided after incorrect choices in the practice.

Training sessions. Participants were trained on the orientation discrimination task with Gabors presented at the same orientation and location throughout training. The stimulus conditions for the first and second trainings were Loc1–Ori1 and Loc2–Ori1, respectively. The orientation (155° or 55°) and location (upper-left or lower-right) of the trained Gabor stimulus were counterbalanced across participants. For the first training at Loc1, each participant was trained for five days with one session in each day. Each session consisted of 16 blocks. For the second training of day 8 at Loc2, each participant was trained for 8 blocks. There was auditory feedback after incorrect choices. The threshold of each training session was determined by the mean of the thresholds from the session.

Reactivation session. The reactivation session was identical to the first training session except that the participants were only trained for 2 blocks.

Tilt discrimination task (TDT). As shown in Figure 1C, each TDT trial began with a 1000 ms fixation interval, followed by the presentation of a Gabor stimulus at Loc2 for 100 ms. The participants were required to judge whether the test stimulus was tilted clockwise or counter-clockwise relative to the vertical with a keyboard within 1500 ms from the offset of the test stimulus. There were five deviations from the vertical: -2.25°, -1.5°, -0.75°, 0°, 0.75°, 1.5°, and

2.25°. There was a practice of 28 trials at the beginning of the TDT session. The formal experiment of the session consisted of 4 blocks, with 140 trials in each block.

Data analysis

The present study focuses on the two trained stimulus conditions (Loc1–Ori1 and Loc2–Ori1) and the influence of reactivation manipulations on the training effects of the two conditions. Therefore, the main results are shown only for these two conditions of interest (referred as Loc1 and Loc2 because they shared the same orientation) to avoid the complexity of conducting too many comparisons in statistics.

Repeated measures two-way ANOVA on threshold, with session (pre-test and mid-test) and location (Loc1 and Loc2) as factors, was performed to examine the effect of the first training. Repeated measures two-way ANOVA on threshold, with session (mid-test and post-test) and location (Loc1 and Loc2) as factors, was performed to examine the effect of the second training.

To reduce the impact of initial threshold on the training effect in between-experiment comparison, we calculated mean percent improvement (MPI) to evaluate the performance improvements between test sessions. $MPI_{pre\text{-}mid}$ was defined as ((pre-test threshold – mid-test threshold)/pre-test threshold) ×100 to measure the improvement from pre-test to mid-test session. $MPI_{mid\text{-}post}$ was defined in a similar fashion for the improvement from mid-test to post-test session. Mixed ANOVAs with experiment as a between-subjects factor and location (Loc1 and Loc2) as a within-subjects factor were performed to compared the training effect across experiments.

Results

Experiment 1

Experiment 1 served as a baseline for the training effect of the procedure (Figure 2A). Training improved participants' discrimination performance, as revealed by the decreased threshold from the first session (mean = 2.36°, SD = 0.629°) to the fifth session (mean = 1.96°, SD = 0.477°) of the training phase (paired *t* test: $t(15) = 4.36$, $p = 0.001$, Cohen's $d = 1.09$). The training effect was further evidenced by the significant main effect of session ($F(1,15) = 53.14$, $p < 0.001$, $\eta_p^2 = 0.78$) when we compared the estimated discrimination thresholds at the trained location (Loc1) and an untrained location reserved for the second training (Loc2) before (pre-test) and after (mid-test) the training sessions. The training effect was largely specific to Loc1 as revealed by the significant interaction between session and location ($F(1,15) = 6.17$, $p = 0.025$, $\eta_p^2 = 0.29$). The thresholds in the two locations were statistically indistinguishable in the pre-test session ($t(15) = 0.48$, $p = 0.64$, Cohen's $d = 0.12$). In mid-test session, the threshold at Loc1 was significantly lower than that of Loc2 ($t(15) = 2.97$, $p = 0.01$, Cohen's $d = 0.74$).

Experiment 2

Experiment 2 introduced a half session training of the same orientation at Loc2 and the results are shown in Figure 2B. The second training was done two days after the first training to ensure that the first training was well-consolidated. The results showed no significant difference from Experiment 1 in the effects of the first training ($F(1,30) = 0.44$, $p = 0.514$, $\eta_p^2 = 0.01$). However, the second training at Loc2 was not effective as neither the threshold difference between the mid-test and post-test sessions ($F(1,15) = 2.41$, $p = 0.141$, $\eta_p^2 = 0.14$) nor

the interaction between session and location ($F(1,15) = 1.68$, $p = 0.215$ $\eta_p^2 = 0.10$) was significant. Also, the threshold changes from the mid-test to post-test sessions were not significantly different between the two experiments ($F(1,30) = 0.01$, $p = 0.928$, $\eta_p^2 < 0.01$). These results revealed a proactive interference effect from the first training to the second training, possibly due to the ten-fold difference in the amount of the training between them.

Experiment 3

In Huang and Li (2022), we showed that conducting a new color-reward learning during the reconsolidation window of the reactivated old color-reward learning facilitated their integration and prevented them from interfering each other. This result agreed with the proposal that high degree of coactivation of two memory traces could lead to their integration and prevent the interference between them (Wammes et al., 2022). Therefore, we conducted Experiment 3 in which a brief reactivation of the first training was added before the second training. This manipulation would potentially induce the coactivation of the two trainings because second training would be temporally overlapped with the reconsolidation window of the first training. Indeed, as shown in Figure 2C, the manipulation resulted in a significant effect for the second training ($F(1,15) = 25.26$, $p < 0.001$, $\eta_p^2 = 0.63$), and this effect was largely specific to Loc2 (significant interaction between session and location: $F(1,15) = 14.17$, $p = 0.002$, $\eta_p^2 = 0.49$). The threshold at Loc1 was statistically lower than that of Loc2 in the mid-test session ($t(15) = 3.75$, $p = 0.002$, Cohen's $d = 0.94$). However, in post-test session, the thresholds at the two locations were statistically indistinguishable ($t(15) = 0.82$, $p = 0.426$, Cohen's $d = 0.21$). Further between-experiments comparisons revealed that the effects of the second training were significantly larger in Experiment 3 as compared with either Experiment 1

($F(1,30) = 14.31$, $p = 0.001$, $\eta_p^2 = 0.32$) or Experiment 2 ($F(1,30) = 18.84$, $p < 0.001$, $\eta_p^2 = 0.39$), suggesting that combining the reactivation with the second training successfully release the inhibition of learning at the previously untrained location (i.e., Loc2). Additionally, the results also revealed that the threshold at Loc1 was further lowered after the second training ($t(15) = 2.76$, $p = 0.015$, Cohen's $d = 0.69$).

Experiment 4

To validate that the coactivation of the two trainings was the key factor in restoring the effect of the second training, we conducted Experiment 4 in which a six-hour interval was placed between the reactivation and second training sessions (Figure 2D). We chose six hours as the time window for the process of reconsolidation based on previous literatures (Bang et al., 2018; Huang et al., 2022; Huang & Li, 2022; Nader et al., 2000). Because the second training was conducted after the first training's reconsolidation, no coactivation of the two trainings would occur and their integration was not possible. The results revealed no significant effect of the second training ($F(1,15) = 1.15$, $p = 0.301$, $\eta_p^2 = 0.07$). The effects of the second training were not significantly different from those of Experiment 2 ($F(1,30) = 1.47$, $p = 0.235$, $\eta_p^2 = 0.05$), but were significantly smaller than those of Experiment 3 ($F(1,30) = 16.34$, $p < 0.001$, $\eta_p^2 = 0.35$). Re-emergence of the proactive interference after introducing this six-hour interval confirmed the important role of reactivation-induced memory integration in Experiment 3.

Experiment 5

We then asked what was the role of location representation in the observed proactive interference in Experiment 2. Simply paying attention to Loc2 seemed not sufficient to solve

the interference because the second training of Experiment 2 directed the participants' attention to Loc2 and yet no learning occurred. It was the learning at Loc2 that was inhibited by the first training, potentially due to the learned low priority of attention during the first training (Wang & Theeuwes, 2018). Experiment 3 demonstrated an effective approach to foster the integration of the two trainings and thus release the inhibition of new learning caused by the intensive first training. Because the two trainings differed only at their stimulus locations, we would expect that the coactivation of the representations of the two locations was a part of the integration process. To test this hypothesis, we conducted Experiment 5 in which a tilt discrimination task at Loc2 was performed immediately after the reactivation and before the six-hour interval. With this setting, any difference in performance change following the second training between Experiments 4 and 5 would be attributed to the addition of the tilt discrimination task. We expected that adding the tilt discrimination task would integrate the two locations and release the inhibition of new learning at Loc2. Indeed, we found that the effects of the second training were restored ($F(1,15) = 17.87$, $p = 0.001$, $\eta_p^2 = 0.54$; Figure 2E), as the training effects were significantly larger than those of Experiment 4 ($F(1,30) = 4.81$, $p = 0.036$, $\eta_p^2 = 0.14$), suggesting that the location-based learned attentional suppression may play an important role in the observed proactive interference. However, the restored effects were significantly smaller than those of Experiment 3 ($F(1,30) = 6.95$, $p = 0.013$, $\eta_p^2 = 0.19$) and there was no further improvement at Loc1 ($t(15) = 0.1$, $p = 0.919$, Cohen's $d = 0.03$) after the second training, suggesting that only location representations were integrated to unlock the inhibition of learning at Loc2 in Experiment 5.

Discussion

Summary of the results across experiments is shown in Figure 3. The reactivation manipulations in Experiments 3 and 5 revealed two related but different results (Figure 3B). In Experiment 3, the reactivation of the first training was immediately before the second training, resulting in significant training effect at Loc2 and additional improvement at Loc1. In Experiment 5, the reactivation of the first training was immediately followed by a tilt discrimination task at Loc2 and the second training was conducted six hours later. The second training could also be protected from the proactive interference in this procedure but the additional performance improvement at Loc1 was not observed. Importantly, the performance improvement from the mid-test to post-test session was smaller in Experiment 5 as compared with that of Experiment 3. We suggest a two-level mechanism of reactivation-induced memory integration to account for these results.

The first level of the mechanism is to release the inhibition of new learning at the previously untrained location (Loc2) by integrating the two locations during the reconsolidation process. This can be achieved by the coactivation of the two locations when the location representation of Loc2 was activated during the reconsolidation window of the reactivated first training at Loc1. In the present study, the representation of Loc2 was activated by the second training and the tilt discrimination task in Experiment 3 and Experiment 5, respectively. Accordingly, we have observed significant improvement at Loc2 following the second training in both experiments. However, only releasing the inhibition of new learning at Loc2 in Experiment 5 was not sufficient to further elevate the performance at Loc1. We would attribute the additional improvement at Loc1 following the second training in Experiment 3 to the

second level of the mechanism. In the second level, the memory traces of the trainings at the two locations were integrated due to their coactivation that occurred when the second training was conducted during the reconsolidation of reactivated first training. This process could form an integrated memory of the two trainings so that training at Loc2 would benefit the performance at both locations as was evident in Experiment 3. Together, these results suggest that which level of the mechanism dominates the reactivation-induced integration process depends on the representations that are coactivated during the reconsolidation.

A recent theory named nonmonotonic plasticity hypothesis (NMPH) suggests that coactivation of two overlapping memories could lead to memory integration or differentiation depending on the level of the coactivation (Ritvo et al., 2019; Wammes et al., 2022). NMPH states that the two memories would be integrated if they are strongly coactivated. Otherwise, if one memory is strongly activated and the unique components of the other memory are moderately active, the coactivation would be moderate one and result in differentiation of the two memories. In Experiment 3, to reactivate the first training, we simply had the participants performing the training task that differed from the second training only at the stimulus location. Hence, the activation of the first training during its reconsolidation was most likely at a high level given the concurrently performed second training. Similarly, the representations of the two locations were also likely to be strongly coactivated in Experiment 5. In both experiments, NMPH would predict the occurrence of integration that agreed with the observed results.

The first training showed partial transfer of learning effect to the untrained location in all experiments ($ps < 0.01$; Figure 3A). This was in sharp contrast with the blocking of the further learning at the untrained location in Experiment 2. Previous studies have shown that the

transfer of learning to untrained locations can be elevated by double training method that was suggested to release the attentional suppression to the untrained location by performing an unrelated task at that location (Wang et al., 2014; Xiao et al., 2008; Zhang et al., 2010). In these studies, the unrelated task was generally performed for several sessions in order to release the learned attentional suppression. This setting was consistent with the results in Experiment 2 in which a short training session at the untrained location was not sufficient to release the inhibition of new learning. However, by adding a brief activation of the first training before the second training, we enabled the new learning at the untrained location and induced further improvement for the first training, demonstrating that reactivation-induced memory integration is a practical way to foster the efficiency of multiple perceptual learnings. Further, our results also validated the idea that reactivation-induced integration could facilitate the generalization of learning (Morton et al., 2017; Ritvo et al., 2019; Schlichting & Frankland, 2017).

Our results suggest an encoding phase hypothesis that the integration occurred during the second training and does not support a retrieval hypothesis that pattern separation was induced by the reactivation so to prevent interference at the retrieval stage. If pattern separation was realized during the reconsolidation process, it would likely to generate two separate associations for the two locations, and thus prevent their interference during the retrieval (Huang et al., 2022). However, the retrieval hypothesis cannot explain the additional performance improvement at Loc1 after the reactivation and second training in Experiment 3. If the two trainings were dissociated during the reconsolidation, the second training would not benefit the performance at the location of the first training. Considering that contextual cueing could facilitate pattern separation and prevent interference of perceptual learning (Huang et al.,

2022), we suggest that both the pattern separation (memory differentiation) and memory integration could help multiple perceptual learnings. The difference was the ways that memory differentiation and memory integration were induced, as contextual cueing could promote the former and reactivation plus new learning promotes the latter.

In summary, the present results suggest a two-level mechanism for reactivation-induced memory integration and its roles in preventing proactive interference in perceptual learning. These findings could be adopted in future applications of various forms of learning that suffer from the interference from previous learning experience.

References

Ahissar, M., & Hochstein, S. (1997). Task difficulty and the specificity of perceptual learning. *Nature*, *387*(6631), 401-406. https://doi.org/10.1038/387401a0

Amar-Halpert, R., Laor-Maayany, R., Nemni, S., Rosenblatt, J. D., & Censor, N. (2017). Memory reactivation improves visual perception. *Nature Neuroscience*, *20*(10), 1325-+. https://doi.org/10.1038/nn.4629

Anderson, M. C. (2003). Rethinking interference theory: Executive control and the mechanisms of forgetting. *Journal of Memory and Language*, *49*(4), 415-445. https://doi.org/10.1016/j.jml.2003.08.006

Ball, K., & Sekuler, R. (1987). Direction-specific improvement in motion discrimination. *Vision Research*, *27*(6), 953-965. https://doi.org/10.1016/0042-6989(87)90011-3

Bang, J. W., Shibata, K., Frank, S. M., Walsh, E. G., Greenlee, M. W., Watanabe, T., & Sasaki, Y. (2018). Consolidation and reconsolidation share behavioural and neurochemical mechanisms. *Nature Human Behaviour*, *2*(7), 507-+. https://doi.org/10.1038/s41562-018-0366-8

Been, M., Jans, B., & De Weerd, P. (2011). Time-Limited consolidation and task Interference: no direct Link. *Journal of Neuroscience*, *31*(42), 14944-14951. https://doi.org/10.1523/jneurosci.1046-11.2011

Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, *10*(4), 433-436. https://doi.org/10.1163/156856897x00357

Chen, C.-Y., & de Beeck, H. O. (2021). Perceptual Learning with Complex Objects: A Comparison between Full-Practice Training and Memory Reactivation. *Eneuro*, *8*(2), Article 0008-19.2021. https://doi.org/10.1523/eneuro.0008-19.2021

Crist, R. E., Kapadia, M. K., Westheimer, G., & Gilbert, C. D. (1997). Perceptual learning of spatial localization: Specificity for orientation, position, and context. *Journal of Neurophysiology*, *78*(6), 2889-2894. https://doi.org/10.1152/jn.1997.78.6.2889

Deveau, J., Ozer, D. J., & Seitz, A. R. (2014). Improved vision and on-field performance in baseball through perceptual learning. *Current Biology*, *24*(4), R146-R147. https://doi.org/10.1016/j.cub.2014.01.004

Donovan, I., & Carrasco, M. (2018). Endogenous spatial attention during perceptual learning facilitates location transfer. *Journal of Vision*, *18*(11), Article 7. https://doi.org/10.1167/18.11.7

Donovan, I., Szpiro, S., & Carrasco, M. (2015). Exogenous attention facilitates location transfer of perceptual learning. *Journal of Vision*, *15*(10), Article 11. https://doi.org/10.1167/15.10.11

Dosher, B. A., & Lu, Z. L. (1998). Perceptual learning reflects external noise filtering and internal noise reduction through channel reweighting. *Proceedings of the National Academy of Sciences of the United States of America*, *95*(23), 13988-13993. https://doi.org/10.1073/pnas.95.23.13988

Dudai, Y. (2006). Reconsolidation: the advantage of being refocused. *Current Opinion in Neurobiology*, *16*(2), 174-178. https://doi.org/10.1016/j.conb.2006.03.010

Elsey, J. W. B., Van Ast, V. A., & Kindt, M. (2018). Human Memory Reconsolidation: A Guiding Framework and Critical Review of the Evidence. *Psychological Bulletin*, *144*(8), 797-848. https://doi.org/10.1037/bul0000152

Fahle, M. (1997). Specificity of learning curvature, orientation, and vernier discriminations. *Vision Research*, *37*(14), 1885-1895. https://doi.org/10.1016/s0042-6989(96)00308-2

Harris, H., Gliksberg, M., & Sagi, D. (2012). Generalized perceptual learning in the absence of sensory adaptation. *Current Biology*, *22*(19), 1813-1817. https://doi.org/10.1016/j.cub.2012.07.059

Herszage, J., & Censor, N. (2017). Memory reactivation enables long-term prevention of interference. *Current Biology*, *27*(10), 1529-+. https://doi.org/10.1016/j.cub.2017.04.025

Herszage, J., & Censor, N. (2018). Modulation of learning and memory: a shared framework for interference and generalization. *Neuroscience*, *392*, 270-280. https://doi.org/10.1016/j.neuroscience.2018.08.006

Hochstein, S., & Ahissar, M. (2002). View from the top: Hierarchies and reverse hierarchies in the visual system. *Neuron*, *36*(5), 791-804. https://doi.org/10.1016/s0896-6273(02)01091-7

Huang, H., Zhang, Y., & Li, S. (2022). Simple contextual cueing prevents retroactive interference in short-term perceptual training of orientation detection tasks. *Attention Perception & Psychophysics*. https://doi.org/10.3758/s13414-022-02520-4

Huang, Z., & Li, S. (2022). Reactivation of learned reward association reduces retroactive interference from new reward learning. *Journal of Experimental Psychology-Learning Memory and Cognition*, *48*(2), 213-225. https://doi.org/10.1037/xlm0000987

Jia, K., Li, Y., Gong, M., Huang, H., Wang, Y., & Li, S. (2021). Perceptual learning beyond perception: mnemonic representation in early visual cortex and intraparietal sulcus. *Journal of Neuroscience*, *41*(20), 4476-4486. https://doi.org/10.1523/jneurosci.2780-20.2021

Jia, K., Xue, X., Lee, J.-H., Fang, F., Zhang, J., & Li, S. (2018). Visual perceptual learning modulates decision network in the human brain: The evidence from psychophysics, modeling, and functional magnetic resonance imaging. *Journal of Vision*, *18*(12), Article 9. https://doi.org/10.1167/18.12.9

Jia, K., Zamboni, E., Kemper, V., Rua, C., Goncalves, N. R., Ng, A. K. T., Rodgers, C. T., Williams, G., Goebel, R., & Kourtzi, Z. (2020). Recurrent processing drives perceptual plasticity. *Current Biology*, *30*(21), 4177-+. https://doi.org/10.1016/j.cub.2020.08.016

Johnston, I. A., Ji, M., Cochrane, A., Demko, Z., Robbins, J. B., Stephenson, J. W., & Green, C. S. (2020). Perceptual learning of appendicitis diagnosis in radiological images. *Journal of Vision*, *20*(8), Article 16. https://doi.org/10.1167/jov.20.8.16

Karni, A., & Sagi, D. (1991). Where practice makes perfect in texture discrimination: Evidence for primary visual cortex plasticity. *Proceedings of the National Academy of Sciences of the United States of America*, *88*(11), 4966-4970. https://doi.org/10.1073/pnas.88.11.4966

Kattner, F., Cochrane, A., Cox, C. R., Gorman, T. E., & Green, C. S. (2017). Perceptual learning generalization from sequential perceptual training as a change in learning rate. *Current Biology*, *27*(6), 840-846. https://doi.org/10.1016/j.cub.2017.01.046

Klorfeld-Auslender, S., Paz, Y., Shinder, I., Rosenblatt, J., Dinstein, I., & Censor, N. (2022). A distinct route for efficient learning and generalization in autism. *Current biology : CB*, *32*(14), 3203-3209.e3203. https://doi.org/10.1016/j.cub.2022.05.059

Law, C. T., & Gold, J. I. (2008). Neural correlates of perceptual learning in a sensory-motor, but not a sensory, cortical area. *Nature Neuroscience*, *11*(4), 505-513.

Lee, J. L. C., Nader, K., & Schiller, D. (2017). An update on memory reconsolidation updating. *Trends in Cognitive Sciences*, *21*(7), 531-545. https://doi.org/10.1016/j.tics.2017.04.006

Morton, N. W., Sherrill, K. R., & Preston, A. R. (2017). Memory integration constructs maps of space, time, and concepts. *Current Opinion in Behavioral Sciences*, *17*, 161-168. https://doi.org/10.1016/j.cobeha.2017.08.007

Nader, K., & Hardt, O. (2009). A single standard for memory: the case for reconsolidation. *Nature*

Reviews Neuroscience, *10*(3), 224-234. https://doi.org/10.1038/nrn2590

Nader, K., Schafe, G. E., & Le Doux, J. E. (2000). Fear memories require protein synthesis in the amygdala for reconsolidation after retrieval. *Nature*, *406*(6797), 722-726. https://doi.org/10.1038/35021052

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, *10*(4), 437-442. https://doi.org/10.1163/156856897x00366

Postman, L., & Underwood, B. J. (1973). Critical issues in interference theory. *Memory & Cognition*, *1*(1), 19-40. https://doi.org/10.3758/bf03198064

Ritvo, V. J. H., Turk-Browne, N. B., & Norman, K. A. (2019). Nonmonotonic plasticity: how memory retrieval drives learning. *Trends in Cognitive Sciences*, *23*(9), 726-742. https://doi.org/10.1016/j.tics.2019.06.007

Sagi, D., & Tanne, D. (1994). Perceptual learning: learning to see. *Current Opinion in Neurobiology*, *4*(2), 195-199. https://doi.org/10.1016/0959-4388(94)90072-8

Schlichting, M. L., & Frankland, P. W. (2017). Memory allocation and integration in rodents and humans. *Current Opinion in Behavioral Sciences*, *17*, 90-98. https://doi.org/10.1016/j.cobeha.2017.07.013

Seitzt, A. R., Yamagishi, N., Werner, B., Goda, N., Kawato, M., & Watanabe, T. (2005). Task-specific disruption of perceptual learning. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(41), 14895-14900. https://doi.org/10.1073/pnas.0505765102

Sha, L. Z., Toh, Y. N., Remington, R. W., & Jiang, Y. V. (2020). Perceptual learning in the identification of lung cancer in chest radiographs. *Cognitive Research-Principles and Implications*, *5*(1), Article 4. https://doi.org/10.1186/s41235-020-0208-x

Shibata, K., Sasaki, Y., Bang, J. W., Walsh, E. G., Machizawa, M. G., Tamaki, M., Chang, L.-H., & Watanabe, T. (2017). Overlearning hyperstabilizes a skill by rapidly making neurochemical processing inhibitory-dominant. *Nature Neuroscience*, *20*(3), 470-475. https://doi.org/10.1038/nn.4490

Shiu, L. P., & Pashler, H. (1992). Improvement in line orientation discrimination is retinally local but dependent on cognitive set. *Perception & Psychophysics*, *52*(5), 582-588. https://doi.org/10.3758/bf03206720

Tamaki, M., Wang, Z., Barnes-Diana, T., Guo, D., Berard, A. V., Walsh, E., Watanabe, T., & Sasaki, Y. (2020). Complementary contributions of non-REM and REM sleep to visual learning. *Nature Neuroscience*, *23*(9), 1150-+. https://doi.org/10.1038/s41593-020-0666-y

Tan, Q., Wang, Z., Sasaki, Y., & Watanabe, T. (2019). Category-Induced Transfer of Visual Perceptual Learning. *Current Biology*, *29*(8), 1374-+. https://doi.org/10.1016/j.cub.2019.03.003

Wammes, J., Norman, K. A., & Turk-Browne, N. (2022). Increasing stimulus similarity drives nonmonotonic representational change in hippocampus. *eLife*, *11*, Article e68344. https://doi.org/10.7554/eLife.68344; 10.7554/eLife.68344.sa1; 10.7554/eLife.68344.sa2

Wang, B., & Theeuwes, J. (2018). Statistical regularities modulate attentional capture independent of search strategy. *Attention Perception & Psychophysics*, *80*(7), 1763-1774. https://doi.org/10.3758/s13414-018-1562-3

Wang, R., Wang, J., Zhang, J.-Y., Xie, X.-Y., Yang, Y.-X., Luo, S.-H., Yu, C., & Li, W. (2016). Perceptual learning at a conceptual Level. *Journal of Neuroscience*, *36*(7), 2238-2246. https://doi.org/10.1523/jneurosci.2732-15.2016

Wang, R., Zhang, J.-Y., Klein, S. A., Levi, D. M., & Yu, C. (2014). Vernier perceptual learning transfers to completely untrained retinal locations after double training: A "piggybacking" effect. *Journal*

of Vision, *14*(13), Article 12. https://doi.org/10.1167/14.13.12

Xiao, L.-Q., Zhang, J.-Y., Wang, R., Klein, S. A., Levi, D. M., & Yu, C. (2008). Complete transfer of perceptual learning across retinal locations enabled by double training. *Current Biology*, *18*(24), 1922-1926. https://doi.org/10.1016/j.cub.2008.10.030

Xiong, Y.-Z., Zhang, J.-Y., & Yu, C. (2016). Bottom-up and top-down influences at untrained conditions determine perceptual learning specificity and transfer. *eLife*, *5*, Article e14614. https://doi.org/10.7554/eLife.14614

Yang, X.-Y., He, Q., & Fang, F. (2022). Transcranial direct current stimulation over the visual cortex facilitates awake consolidation of visual perceptual learning. *Brain Stimulation*, *15*(2), 380-382. https://doi.org/10.1016/j.brs.2022.01.019

Yotsumoto, Y., Chang, L.-h., Watanabe, T., & Sasaki, Y. (2009). Interference and feature specificity in visual perceptual learning. *Vision Research*, *49*(21), 2611-2623. https://doi.org/10.1016/j.visres.2009.08.001

Zhang, J.-Y., Zhang, G.-L., Xiao, L.-Q., Klein, S. A., Levi, D. M., & Yu, C. (2010). Rule-Based Learning Explains Visual Perceptual Learning and Its Specificity and Transfer. *Journal of Neuroscience*, *30*(37), 12323-12328. https://doi.org/10.1523/jneurosci.0704-10.2010

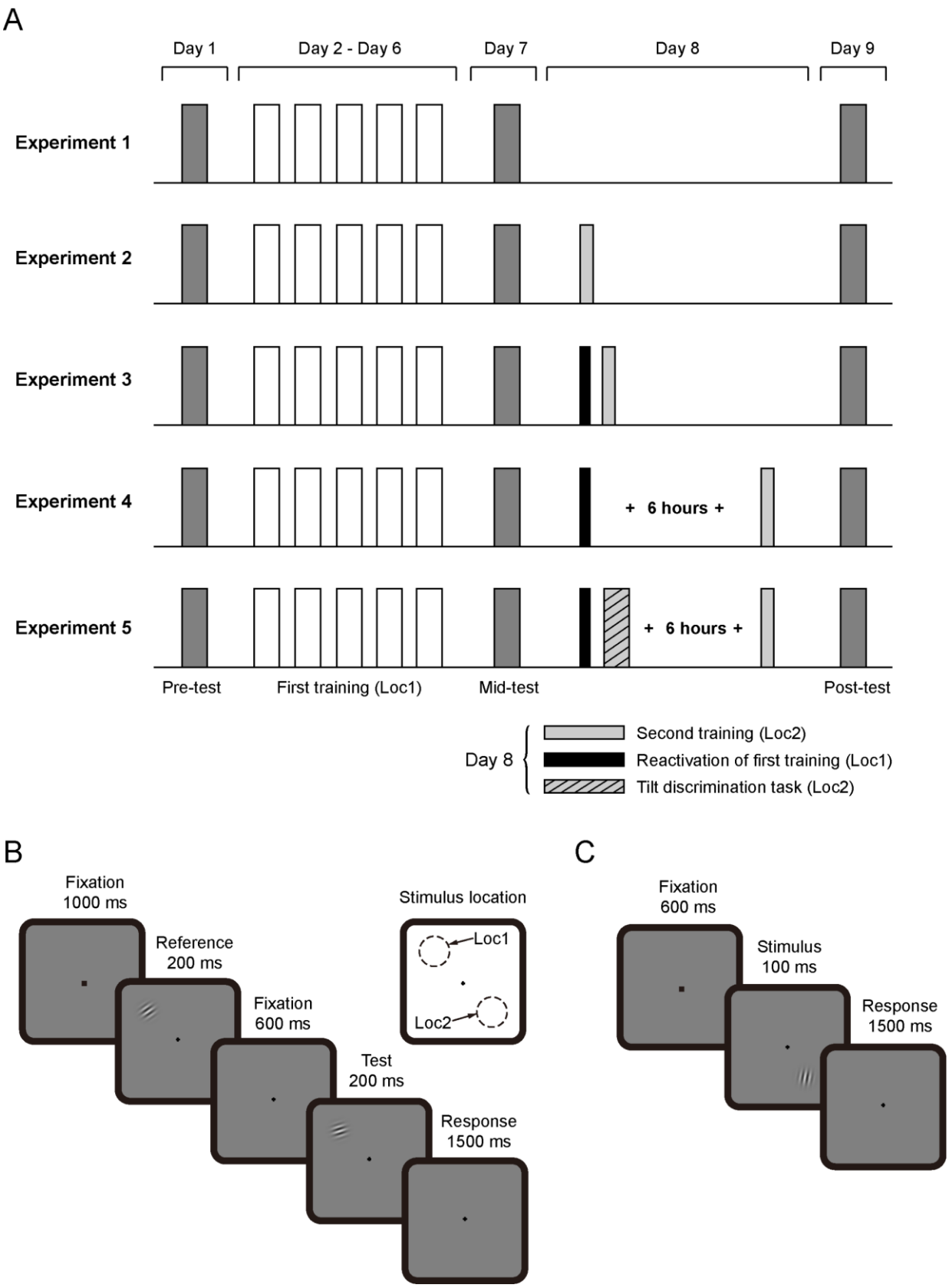

Figure 1. Experimental design. (A) Procedures of the experiments. (B) Orientation discrimination task. (C) Tilt discrimination task.

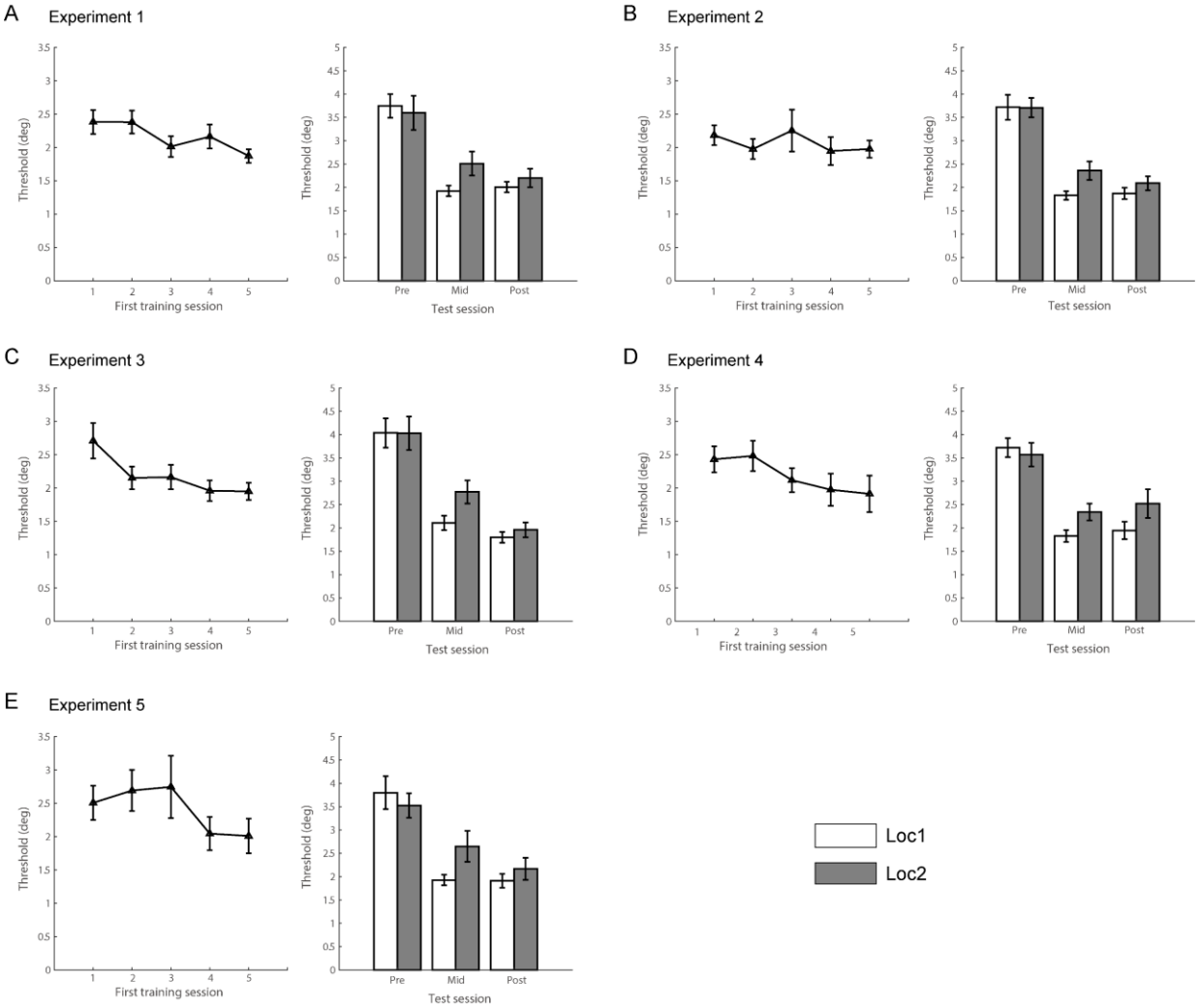

Figure 2. Behavioral results for the first training sessions (left panel) and test sessions (right panels). (A) Experiment 1. (B) Experiment 2. (C) Experiment 3. (D) Experiment 4. (E) Experiment 5. Error bars represent standard errors.

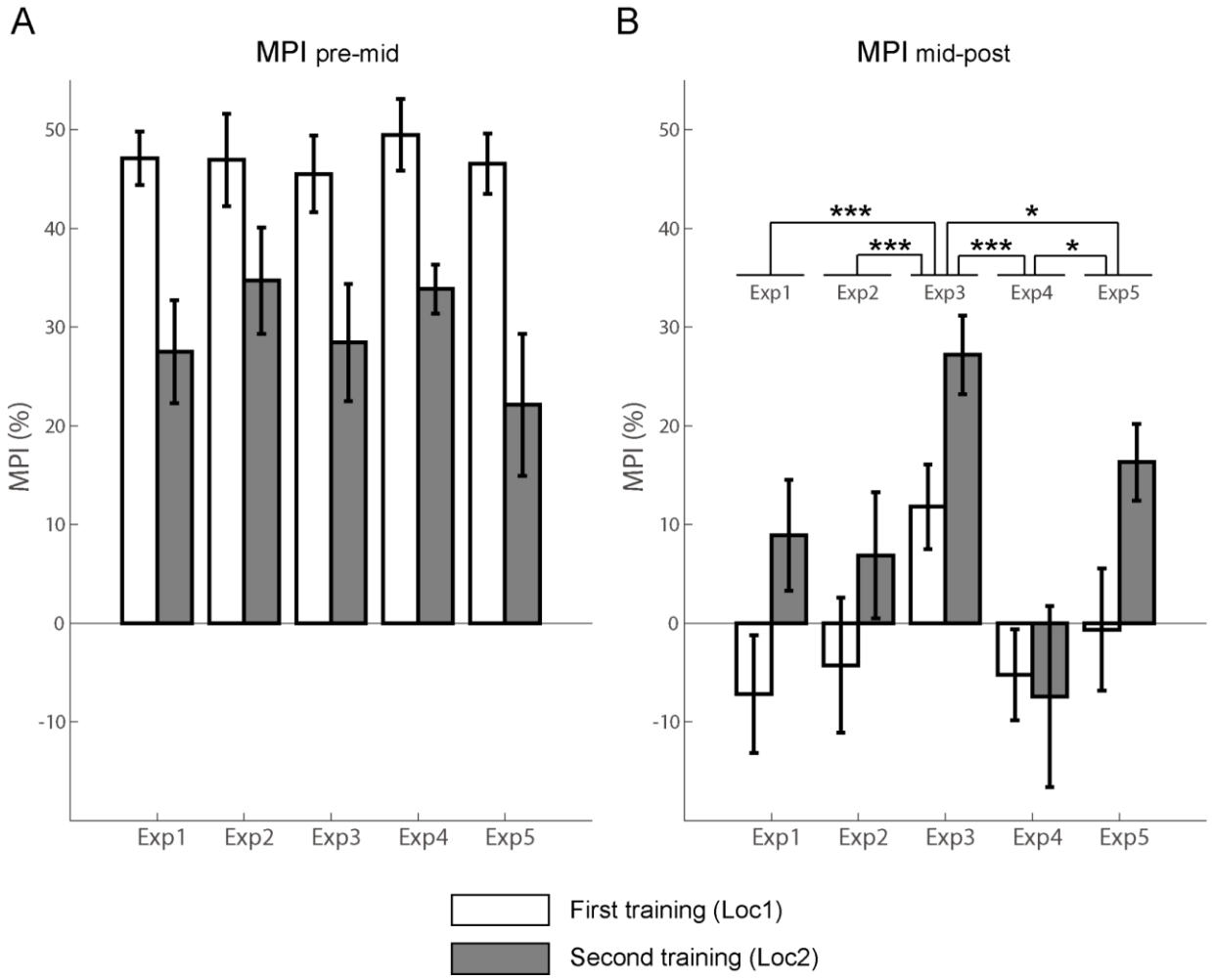

Figure 3. Summary of the results. Mean percent improvements (MPIs) after the (A) first training ($MPI_{pre\text{-}mid}$) and (B) second training ($MPI_{mid\text{-}post}$) are shown for each experiment. Error bars represent standard errors. * $p < 0.05$, *** $p < 0.001$.