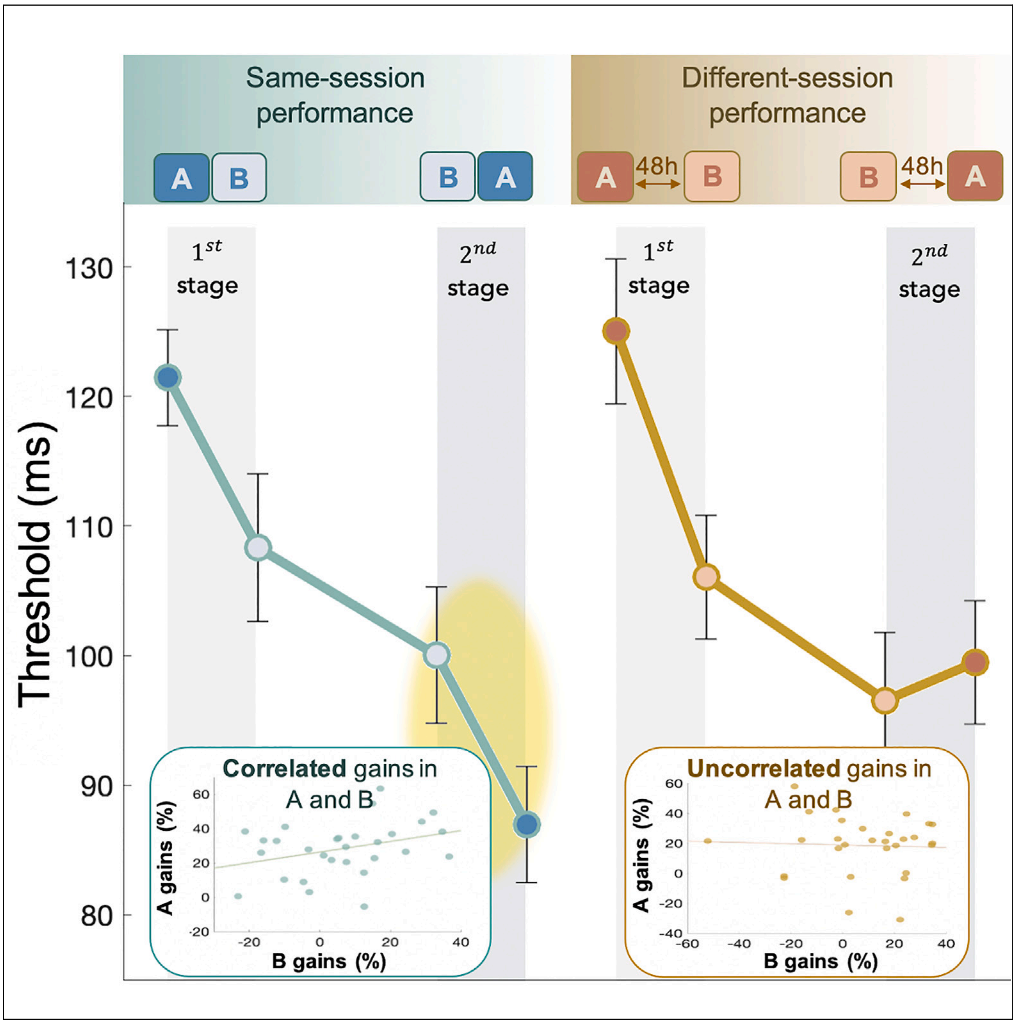
iScience

CellPress
OPEN ACCESS

Article

Modulating temporal dynamics of performance across retinotopic locations enhances the generalization of perceptual learning



Taly Kondat, Maya Aderka, Nitzan Censor

censornitzan@tauex.tau.ac.il

Highlights

Perceptual learning, often specific to trained conditions, limits generalization

Temporal proximity of different retinotopic locations enhanced generalization

Learning was correlated across locations, suggesting integrated learning mechanisms

Kondat et al., iScience 26, 108276
November 17, 2023
https://doi.org/10.1016/j.isci.2023.108276

iScience

CellPress
OPEN ACCESS

Article

Modulating temporal dynamics of performance across retinotopic locations enhances the generalization of perceptual learning

Taly Kondat,[1] Maya Aderka,[1] and Nitzan Censor[1,2,3,*]

SUMMARY

Human visual perception can be improved through perceptual learning. However, such learning is often specific to stimulus and learning conditions. Here, we explored how temporal dynamics of performance across conditions impact learning generalization. Participants performed a visual task, with the target at retinotopic location A. Then, the target was presented at location B either immediately after location A (same-session performance) or following a 48h consolidation period (different-session performance). Long-term generalization was measured the following week. Following initial training, both groups demonstrated generalization, consistent with previous accounts of fast learning. However, long-term generalization was enhanced in the same-session performance group. Consistently, improvements at locations A and B were correlated only following same-session performance, implying an integrated learning process across locations. The results support a new account of perceptual learning and generalization dynamics, suggesting that the temporal proximity of learning and consolidation of different conditions may integrate correlated learning processes, facilitating generalized learning.

INTRODUCTION

Acquiring a new skill often results in long-term learning, which can be highly beneficial when learning is generalized to untrained conditions. While the generalization of learning is often observed across tasks, perceptual learning has commonly been documented as an interesting exception. Visual perceptual learning leads to an increase in visual sensitivity following practice.[1–3] Moreover, studies have shown that the learned visual skill persists for months and years.[4,5] However, a remarkable restriction often observed in perceptual learning, is its strong specificity to the trained stimuli properties and learning conditions (e.g., orientation, trained eye, and retinal location).[3,5–10]

Although specificity has been identified with perceptual learning, during recent years transfer of perceptual learning has been shown under certain conditions,[11–17] implying that specificity is not necessarily predetermined.

Perceptual learning, such as other procedural skills, relies distinctively on offline consolidation, the process in which fragile memory traces are stabilized.[18] During consolidation neurobiological changes, which are induced with training, are balanced, ultimately transforming the newly acquired memory into a steady long-term form.[19–25] These changes require a post-acquisition temporal interval of rest to take place[26,27] and are commonly associated with specific stages of sleep.[23,28–32]

These memory stabilization processes have been found to induce positive influences on perceptual learning. Improved behavioral outcomes such as offline performance gains[4,5,33–35] and resistance to within-session deterioration[36] have been observed when a time period including overnight sleep is allowed between learning sessions. Studies have shown that neural activity during post-acquisition sleep is correlated with offline gains[34,37] and that interference with the consolidation process by repetitive transcranial magnetic stimulation (rTMS) to the trained visual cortex led to impaired performance on the following day.[38,39]

Nevertheless, for certain learning outcomes, such as the ability to generalize learning to untrained conditions, where flexibility is necessary, it is possible that the stabilization of the acquired memory might have counteractive effects. We hypothesized that same-session performance across learning conditions, potentially inducing integrated memory stabilization processes for both conditions, will enhance the generalization of learning. To test this hypothesis, participants performed the texture discrimination task (TDT; Figure 1A) with the target stimulus appearing in retinotopic location A. Then, the task was performed with the target stimulus in retinotopic location B either immediately after the performance at location A (same-session performance) or following a 48h consolidation period (different-session performance; Figure 1B). To evaluate long-term learning and generalization, performance in both locations was similarly tested the following week.

[1]Sagol School of Neuroscience, Tel Aviv University, Tel Aviv 69978, Israel
[2]School of Psychological Sciences, Tel Aviv University, Tel Aviv 69978, Israel
[3]Lead contact
*Correspondence: censornitzan@tauex.tau.ac.il
https://doi.org/10.1016/j.isci.2023.108276

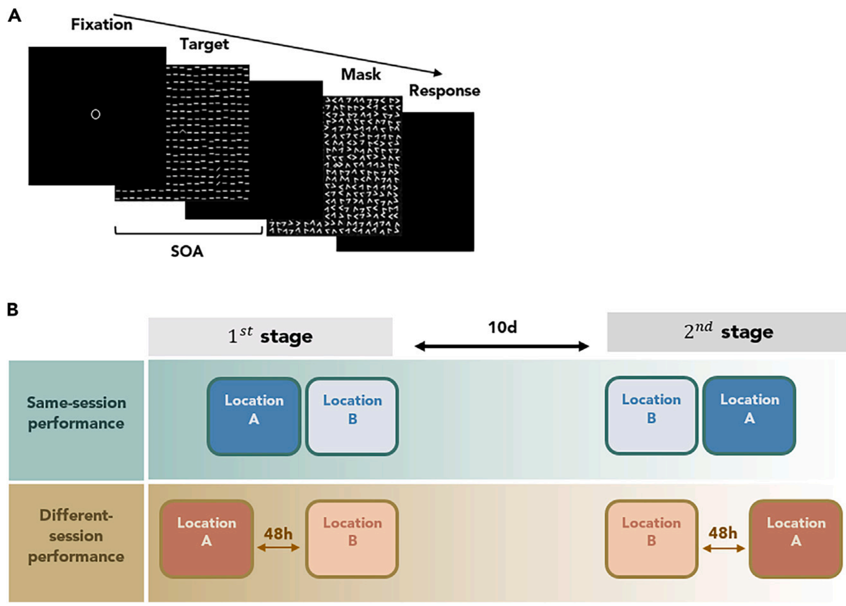


Figure 1. Texture discrimination task (TDT) and experimental procedure

(A) TDT example trial. Observers were required to discriminate between a horizontal or vertical orientation of a peripheral target consisting of three diagonal bars appearing for 10ms. Fixation was enforced by a forced-choice letter discrimination task (rotated T or L) at the center of the display and was followed by auditory feedback for incorrect discrimination. The target-to-mask asynchrony (SOA, measured from the onset of the target to the onset of the mask) varied within the session to obtain a psychometric curve, from which the SOA discrimination threshold was derived.

(B) Experimental procedure. In the first stage of the experiment, participants completed 252 trials with the target stimulus presented in retinotopic location A (UL or LR, condition A), followed by 252 trials in a different retinotopic location B (LR or UL, respectively, condition B). The conditions were conducted either within the same session (same-session performance), or with an interval of 48h between them (different-session performance). In the second stage of the experiment, following 10 days, long-term effects were measured in both retinotopic locations. Here also, location A was measured immediately after location B in the same-session performance group, or following 48h in the different-session performance group.

RESULTS

Initial improvements

In the first stage of the experiment, significant improvement was observed between retinotopic locations A and B across experimental groups (mean improvement 16.04 $\pm$ 5.01 ms SE; $F_{1,55}$ = 20.97, p < 0.001, partial η^2 = 0.276), with no between-group interaction (location $\times$ group $F_{1,55}$ = 0.39, p = 0.53, partial η^2 = 0.007; same-session mean improvement 13.10 $\pm$ 7.28 ms; different-session mean improvement 18.98 $\pm$ 6.96 ms; Figure 2A). These results indicate learning generalization at an early stage of the learning processes.

Long-term improvements

We then continued to test long-term learning, from the first to the second stage of the experiment (Figure 2A). The results showed long-term improvement across groups (mean location B improvement 7.17% $\pm$ 2.47%, t_{57} = 2.90, p = 0.005, Cohen's d = 0.380, note that quantifying learning within the same location enables using percent change, a more sensitive measure accounting for between-subject variability). Of note, this moderate learning magnitude may result from two consecutive sessions separated more than a week apart, similar to previous studies,[40] and in contrast to multiple sessions separated by shorter time intervals.[1,41–43] Consistently, ten participants from each group did not exhibit offline gains at this interval of the experiment, and although the distribution varied, no prominent difference in learning magnitude was observed between the groups (same-session group 6.43% $\pm$ 3.09%, different-session group 7.90% $\pm$ 3.92%; $F_{3,54}$ = 2.62, p = 0.06, *partial* η^2 = 0.127).

Interestingly, generalization at the second, long-term stage of the experiment was enhanced following same-session performance (mean improvement 13.05 $\pm$ 5.74 ms) compared to different-session performance (mean improvement −2.92 $\pm$ 6.11 ms), with a significant location $\times$ group interaction ($F_{1,55}$ = 5.37, p = 0.024, partial η^2 = 0.089; Figure 2B). This was further confirmed by testing overall learning at location A, which was significantly greater ($F_{3,54}$ = 4.16, p = 0.010, *partial* η^2 = 0.188) in the same-session performance group (mean improvement 28.37% $\pm$ 2.90%) compared to the different-session performance group (mean improvement 18.54% $\pm$ 3.62%). These results reveal enhanced learning generalization following same-session performance, suggesting that modulating temporal dynamics across learning conditions facilitates learning generalization.

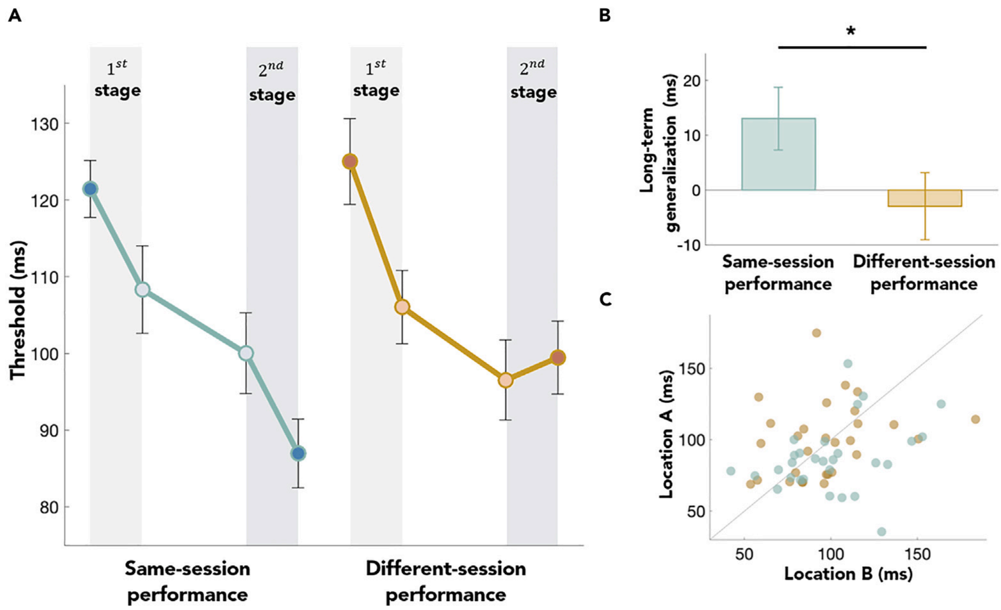


Figure 2. Learning curves and long-term generalization

(A) Mean discrimination thresholds for both same-session and different-session performance groups. Thresholds were measured from locations A (first and fourth points) and B (second and third points) at the first and second stages of the experiment.

(B) Long-term generalization (improvement at the second stage of the experiment between the two locations).

(C) Single-subject threshold at location B versus location A of the same-session (green) and different-session (yellow) performance groups at the second stage of the experiment, presented in a scatterplot along a unit slope line (y = x). Each point represents a participant. Data accumulating below the unit line reflect participants who expressed long-term generalization gains. *$p < 0.05$. Error bars represent SE.

Correlation between improvements in retinotopic locations A and B

Finally, there was a linear correlation between the learning magnitude at location A and location B in the same-session performance group ($r = 0.33$, $p = 0.039$; Figure 3A). No such correlation was observed in the different-session performance group ($r = -0.05$, $p = 0.41$; Figure 3B). Thus, consistent with the above generalization results, the findings showing that improvements at locations A and B were correlated following same-session performance may imply an integrated learning process across both locations.

DISCUSSION

The aim of this study was to examine whether modulating the temporal dynamics of performance across learning conditions impacts the generalization of learning. The results show that performing the task with two target retinotopic locations immediately one after the other (same-session performance), enhances long-term generalization. This was in contrast to when the two target retinotopic locations were performed in different sessions (different-session performance), separated by a 48h consolidation period. Consistently, long-term improvements in the two retinotopic locations were correlated following same-session, but not different-session performance, potentially implying an integrated learning process across both locations. Short-term generalization and subsequent learning remained comparable across groups.

Generalization of learning is often a highly desirable outcome of the learning process, promoting learning efficiency beyond the specific trained features. However, perceptual learning is known for its strong specificity, with learning gains commonly showing minimal transfer to untrained conditions.[3,5–10] This remarkable limitation has led to a substantial challenge aimed to unlock this specificity and enhance learning generalization.[44]

The results of the current study show that performing the task with two target retinotopic locations one after the other (same-session group) enhances long-term performance at location A. This was evident in (1) enhanced improvement between location B and location A at the second stage of the experiment and (2) an additional analysis showing enhanced overall learning at location A. Therefore, final performance at location A in the same-session group may have benefited from both the initial learning at location A, as well as additional practice at location B. Together with the results showing that long-term improvements in both retinotopic locations are correlated, this may point to an integrated learning process across both locations. In contrast, when the task is performed with each target retinotopic location on separate days, it is conceivable that one condition undergoes consolidation first, and that such stabilization limits long-term generalization. These findings may be consistent with previous studies showing improved generalization following reduced training duration,[36,45–47] avoiding over-exposure to specific task conditions,[48] and increasing training variability.[49,50] Commonly these mechanisms are thought to prevent sensory adaptation which may lead to overfitting.[44,51]

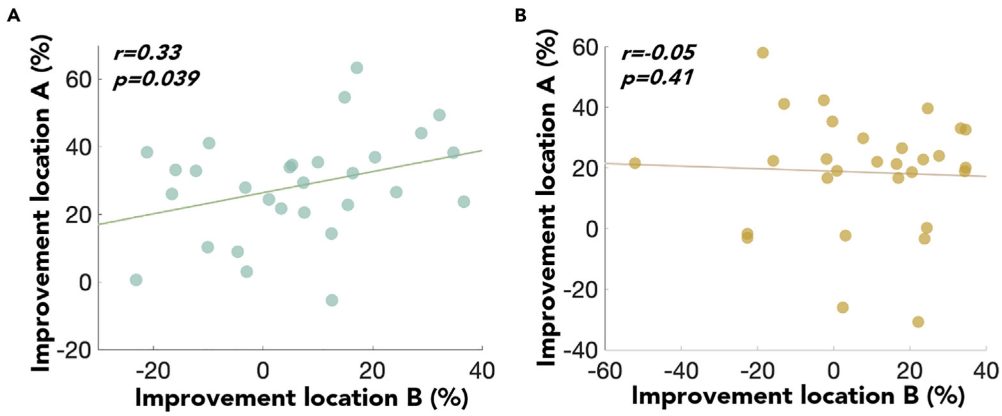


Figure 3. Correlation between long-term improvement at locations B and A

(A) Same-session performance and (B) Different-session performance groups. Long-term improvements at locations B and A were correlated in the same-session performance group, suggesting an integrated learning process across conditions.

Consistently, same-session performance of different retinotopic target locations may reduce the effects of such overfitting by preventing the stabilization of learning in one location before learning the other, and thus enhance generalization as shown here.

Studies have described changes in the communication between early visual and higher-order attention and decision areas following perceptual learning.[52,53] One such mechanism suggests changes in readout weights between early visual representation and higher-ordered regions, resulting in a reduction of noise.[54,55] Accordingly, it is possible that when same-session performances across different locations can consolidate simultaneously, the reweighted readout of both locations to the higher-order regions may function as a unified network. If true, then when one connection is active again, the weights of the inactive readout are enhanced as well. This idea is also consistent with the findings indicating a correlation between the two conditions' long-term improvements.

The results of the current study may also have implications regarding the link between pre-tests and subsequent generalization.[15,42,56,57] In addition, when following pretest at location A, location B is repeatedly trained over multiple consecutive days,[15] generalization of location A is diminished by extensive practice at location B. This may be consistent with overfitting frameworks discussed above.[36,44,46–50]

Noteworthy, in accordance with previous findings demonstrating "fast learning" mechanisms during initial training,[4,58] the present results showed early generalization in both groups, irrespective of the performance temporal proximity. These mechanisms suggest that general aspects of the task are learned at an early stage of the learning process and can be generalized to untrained conditions, possibly by engaging higher-order brain regions.[53] Here, in addition to these previously documented early generalization effects, the results show unique long-term generalization. This long-term generalization is dissociated from early-stage generalization, as evident in the different-session group which showed fast but not long-term generalization. This dissociation between early and late stage mechanisms may be consistent with the two-stage model previously proposed in perceptual learning.[53,59]

In sum, the results show that modulating temporal dynamics of integrated learning conditions considerably enhances the generalization of perceptual learning. As such, the results may support a new account of perceptual learning and generalization dynamics, providing important insights for future applications geared to modulate the specificity-generalization balance and optimize learning outcomes.

Limitations of the study

While previous studies have documented generalization to untested locations,[48,50] the current study examined generalization to a previously tested location. Testing a new location C within our framework may not result in complete generalization, since the main mechanism here relates to the integrated learning of previously tested locations A and B. This mechanism possibly differs from inserting variability into the learning sessions which may reduce the induction of adaptation, an additional important mechanism enhancing generalization.[48,50]

Of note, the results showing no long-term generalization gains from location B to location A in the different-session group may be related to interference effects.[60–63] As such, an additional consolidation cycle may have stabilized location B performance, interfering with subsequent location A performance. Nevertheless, previous interference studies have commonly documented interference when tasks are performed on the same day, with no consolidation interval between them and in the same retinotopic location.[64,65] Thus, future studies could be designed to further test interference effects on different session performances.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- RESOURCE AVAILABILITY

ACKNOWLEDGMENTS

The study was supported by the European Research Council (ERC-2019-COG 866093).

Taly Kondat is a fellow of the Ariane de Rothschild Women Doctoral Program.

AUTHOR CONTRIBUTIONS

T.K. and N.C. designed the study. T.K. and M.A. performed the research. T.K. analyzed the data. T.K. and N.C. wrote the article.

DECLARATION OF INTERESTS

The authors declare no competing interests.

Received: August 10, 2023
Revised: September 28, 2023
Accepted: October 17, 2023
Published: October 19, 2023

REFERENCES

1. Karni, A., and Sagi, D. (1991). Where practice makes perfect in texture discrimination: evidence for primary visual cortex plasticity. Proc. Natl. Acad. Sci. USA *88*, 4966–4970. https://doi.org/10.1073/pnas.88.11.4966.
2. Poggio, T., and Fahle, M. (2002). Perceptual Learning (MIT Press).
3. Schwartz, S., Maquet, P., and Frith, C. (2002). Neural correlates of perceptual learning: A functional MRI study of visual texture discrimination. Proc. Natl. Acad. Sci. USA *99*, 17137–17142. https://doi.org/10.1073/pnas.1030820100.
4. Karni, A., and Sagi, D. (1993). The time course of learning a visual skill. Nature *365*, 250–252. https://doi.org/10.1038/365250a0.
5. Schoups, A.A., Vogels, R., and Orban, G.A. (1995). Human perceptual learning in identifying the oblique orientation: retinotopy, orientation specificity and monocularity. J. Physiol. *483*, 797–810. https://doi.org/10.1113/jphysiol.sp020623.
6. Crist, R.E., Kapadia, M.K., Westheimer, G., and Gilbert, C.D. (1997). Perceptual Learning of Spatial Localization: Specificity for Orientation, Position, and Context. J. Neurophysiol. *78*, 2889–2894. https://doi.org/10.1152/jn.1997.78.6.2889.
7. Fahle, M. (1997). Specificity of learning curvature, orientation, and vernier discriminations. Vis. Res. *37*, 1885–1895. https://doi.org/10.1016/S0042-6989(96)00308-2.
8. Saffell, T., and Matthews, N. (2003). Task-specific perceptual learning on speed and direction discrimination. Vis. Res. *43*, 1365–1374. https://doi.org/10.1016/S0042-6989(03)00137-8.
9. Watanabe, T., Náñez, J.E., Sr., Koyama, S., Mukai, I., Liederman, J., and Sasaki, Y. (2002). Greater plasticity in lower-level than higher-level visual motion processing in a passive perceptual learning task. Nat. Neurosci. *5*, 1003–1009. https://doi.org/10.1038/nn915.
10. Yu, C., Klein, S.A., and Levi, D.M. (2004). Perceptual learning in contrast discrimination and the (minimal) role of context. J. Vis. *4*, 169–182. https://doi.org/10.1167/4.3.4.
11. Aberg, K.C., Tartaglia, E.M., and Herzog, M.H. (2009). Perceptual learning with Chevrons requires a minimal number of trials, transfers to untrained directions, but does not require sleep. Vision Res. *49*, 2087–2094. https://doi.org/10.1016/j.visres.2009.05.020.
12. Jeter, P.E., Dosher, B.A., Petrov, A., and Lu, Z.L. (2009). Task precision at transfer determines specificity of perceptual learning. J. Vis. *9*, 1.1–1.13. https://doi.org/10.1167/9.3.1.
13. Liu, Z., and Weinshall, D. (2000). Mechanisms of generalization in perceptual learning. Vision Res. *40*, 97–109. https://doi.org/10.1016/S0042-6989(99)00140-6.
14. Snell, N., Kattner, F., Rokers, B., and Green, C.S. (2015). Orientation transfer in vernier and stereoacuity training. PLoS One *10*, e0145770. https://doi.org/10.1371/journal.pone.0145770.
15. Xiao, L.Q., Zhang, J.Y., Wang, R., Klein, S.A., Levi, D.M., and Yu, C. (2008). Complete Transfer of Perceptual Learning across Retinal Locations Enabled by Double Training. Curr. Biol. *18*, 1922–1926. https://doi.org/10.1016/j.cub.2008.10.030.
16. Zhang, J.Y., Zhang, G.L., Xiao, L.Q., Klein, S.A., Levi, D.M., and Yu, C. (2010). Rule-Based Learning Explains Visual Perceptual Learning and Its Specificity and Transfer. J. Neurosci. *30*, 12323–12328. https://doi.org/10.1523/JNEUROSCI.0704-10.2010.
17. Zhang, T., Xiao, L.Q., Klein, S.A., Levi, D.M., and Yu, C. (2010). Decoupling location specificity from perceptual learning of orientation discrimination. Vis. Res. *50*, 368–374. https://doi.org/10.1016/j.visres.2009.08.024.
18. Dudai, Y., Karni, A., and Born, J. (2015). The Consolidation and Transformation of Memory. Neuron *88*, 20–32. https://doi.org/10.1016/j.neuron.2015.09.004.
19. Abel, T., and Lattal, K.M. (2001). Molecular mechanisms of memory acquisition, consolidation and retrieval. Curr. Opin. Neurobiol. *11*, 180–187. https://doi.org/10.1016/S0959-4388(00)00194-X.
20. Dudai, Y. (2004). The neurobiology of consolidations, or, how stable is the engram? Annu. Rev. Psychol. *55*, 51–86. https://doi.org/10.1146/annurev.psych.55.090902.142050.
21. Dudai, Y. (2012). The restless engram: Consolidations never end. Annu. Rev. Neurosci. *35*, 227–247. https://doi.org/10.1146/annurev-neuro-062111-150500.
22. Miyamoto, D. (2023). Neural circuit plasticity for complex non-declarative sensorimotor memory consolidation during sleep. Neurosci. Res. *189*, 37–43. https://doi.org/10.1016/j.neures.2022.12.020.
23. Tononi, G., and Cirelli, C. (2014). Sleep and the Price of Plasticity: From Synaptic and Cellular Homeostasis to Memory Consolidation and Integration. Neuron *81*, 12–34. https://doi.org/10.1016/j.neuron.2013.12.025.
24. Tononi, G., and Cirelli, C. (2016). Sleep and Synaptic Down-Selection. In Micro-, Meso- and Macro-Dynamics of the Brain. Buzsáki G., and Christen Y. (Springer International Publishing AG), pp. 99–106. https://doi.org/10.1007/978-3-319-28802-4.

25. Klinzing, J.G., Niethard, N., and Born, J. (2019). Mechanisms of systems memory consolidation during sleep. Nat. Neurosci. *22*, 1598–1610. https://doi.org/10.1038/s41593-019-0467-3.
26. Wamsley, E.J. (2022). Offline memory consolidation during waking rest. Nat. Rev. Psychol. *1*, 441–453. https://doi.org/10.1038/s44159-022-00072-w.
27. Wang, S.Y., Baker, K.C., Culbreth, J.L., Tracy, O., Arora, M., Liu, T., Morris, S., Collins, M.B., and Wamsley, E.J. (2021). "Sleep-dependent" memory consolidation? Brief periods of post-training rest and sleep provide an equivalent benefit for both declarative and procedural memory. Learn. Mem. *28*, 195–203. https://doi.org/10.1101/LM.053330.120.
28. Stickgold, R. (2005). Sleep-dependent memory consolidation. Nature *437*, 1272–1278. https://doi.org/10.1038/nature04286.
29. Tamaki, M., Wang, Z., Barnes-Diana, T., Guo, D., Berard, A.V., Walsh, E., Watanabe, T., and Sasaki, Y. (2020). Complementary contributions of non-REM and REM sleep to visual learning. Nat. Neurosci. *23*, 1150–1156. https://doi.org/10.1038/s41593-020-0666-y.
30. Tononi, G., and Cirelli, C. (2006). Sleep function and synaptic homeostasis. Sleep Med. Rev. *10*, 49–62. https://doi.org/10.1016/j.smrv.2005.05.002.
31. Walker, M.P., and Stickgold, R. (2005). It's practice, with sleep, that makes perfect: Implications of sleep-dependent learning and plasticity for skill performance. Clin. Sports Med. *24*, 301–317. https://doi.org/10.1016/j.csm.2004.11.002.
32. Stickgold, R., James, L., and Hobson, J.A. (2000). Visual Discrimination Learning Requires Sleep after Training. Nat. Neurosci. *3*, 1237–1238. https://doi.org/10.1080/07294360.2015.1107885.
33. Gervan, P., and Kovacs, I. (2010). Two phases of offline learning in contour integration. J. Vis. *10*, 24. https://doi.org/10.1167/10.6.24.
34. Tamaki, M., Wang, Z., Watanabe, T., and Sasaki, Y. (2018). Trained-feature specific offline learning in an orientation detection task. J. Vis. *19*, 12. https://doi.org/10.1101/429761.
35. Walker, M.P. (2005). A refined model of sleep and the time course of memory formation. Behav. Brain Sci. *28*, 51–64. , discussion 64-104. https://doi.org/10.1017/S0140525X05000026.
36. Censor, N., and Sagi, D. (2008). Benefits of efficient consolidation: Short training enables long-term resistance to perceptual adaptation induced by intensive testing. Vis. Res. *48*, 970–977. https://doi.org/10.1016/j.visres.01.016.
37. Yotsumoto, Y., Sasaki, Y., Chan, P., Vasios, C.E., Bonmassar, G., Ito, N., Náñez, J.E., Sr., Shimojo, S., and Watanabe, T. (2009). Location-Specific Cortical Activation Changes during Sleep after Training for Perceptual Learning. Curr. Biol. *19*, 1278–1282. https://doi.org/10.1016/j.cub.2009.06.011.
38. de Weerd, P., Reithler, J., van de Ven, V., Been, M., Jacobs, C., and Sack, A.T. (2012). Posttraining transcranial magnetic stimulation of striate cortex disrupts consolidation early in visual skill learning. J. Neurosci. *32*, 1981–1988. https://doi.org/10.1523/JNEUROSCI.3712-11.2011.
39. Shmuel, D., Frank, S.M., Sharon, H., Sasaki, Y., Watanabe, T., and Censor, N. (2021). Early Visual Cortex Stimulation Modifies Well-Consolidated Perceptual Gains. Cerebr. Cortex *31*, 138–146. https://doi.org/10.1093/cercor/bhaa215.
40. Amar-Halpert, R., Laor-Maayany, R., Nemni, S., Rosenblatt, J.D., and Censor, N. (2017). Memory reactivation improves visual perception. Nat. Neurosci. *20*, 1325–1328. https://doi.org/10.1038/nn.4629.
41. Yotsumoto, Y., Watanabe, T., and Sasaki, Y. (2008). Different Dynamics of Performance and Brain Activation in the Time Course of Perceptual Learning. Neuron *57*, 827–833. https://doi.org/10.1016/j.neuron.2008.02.034.
42. Harris, H., and Sagi, D. (2015). Effects of spatiotemporal consistencies on visual learning dynamics and transfer. Vis. Res. *109*, 77–86. https://doi.org/10.1016/j.visres.2015.02.013.
43. Kang, D.W., Kim, D., Chang, L.H., Kim, Y.H., Takahashi, E., Cain, M.S., Watanabe, T., and Sasaki, Y. (2018). Structural and Functional Connectivity Changes beyond Visual Cortex in a Later Phase of Visual Perceptual Learning. Sci. Rep. *8*, 5186–5189. https://doi.org/10.1038/s41598-018-23487-z.
44. Sagi, D. (2011). Perceptual learning in Vision Research. Vis. Res. *51*, 1552–1566. https://doi.org/10.1016/j.visres.2010.10.019.
45. Censor, N., and Sagi, D. (2009). Global resistance to local perceptual adaptation in texture discrimination. Vis. Res. *49*, 2550–2556. https://doi.org/10.1016/j.visres.2009.03.018.
46. Hung, S.C., and Seitz, A.R. (2014). Prolonged Training at Threshold Promotes Robust Retinotopic Specificity in Perceptual Learning. J. Neurosci. *34*, 8423–8431. https://doi.org/10.1523/JNEUROSCI.0745-14.2014.
47. Jeter, P.E., Dosher, B.A., Liu, S.H., and Lu, Z.L. (2010). Specificity of perceptual learning increases with increased training. Vis. Res. *50*, 1928–1940. https://doi.org/10.1016/j.visres.2010.06.016.
48. Harris, H., Gliksberg, M., and Sagi, D. (2012). Generalized Perceptual Learning in the Absence of Sensory Adaptation. Curr. Biol. *22*, 1813–1817. https://doi.org/10.1016/j.cub.2012.07.059.
49. Hussain, Z., Bennett, P.J., and Sekuler, A.B. (2012). Versatile perceptual learning of textures after variable exposures. Vis. Res. *61*, 89–94. https://doi.org/10.1016/j.visres.2012.01.005.
50. Manenti, G.L., Dizaji, A.S., and Schwiedrzik, C.M. (2023). Variability in training unlocks generalization in visual perceptual learning through invariant representations. Curr. Biol. *33*, 817–826.e3. https://doi.org/10.1016/j.cub.2023.01.011.
51. Censor, N., Harris, H., and Sagi, D. (2016). A dissociation between consolidated perceptual learning and sensory adaptation in vision. Sci. Rep. *6*, 38819. https://doi.org/10.1038/srep38819.
52. Maniglia, M., and Seitz, A.R. (2018). Towards a whole brain model of Perceptual Learning. Curr. Opin. Behav. Sci. *20*, 47–55. https://doi.org/10.1016/j.cobeha.2017.10.004.
53. Watanabe, T., and Sasaki, Y. (2015). Perceptual Learning: Toward a Comprehensive Theory. Annu. Rev. Psychol. *66*, 197–221. https://doi.org/10.1146/annurev-psych-010814-015214.
54. Dosher, B.A., and Lu, Z.L. (1998). Perceptual learning reflects external noise filtering and internal noise reduction through channel reweighting. Proc. Natl. Acad. Sci. USA *95*, 13988–13993. https://doi.org/10.1073/pnas.95.23.13988.
55. Dosher, B.A., Jeter, P., Liu, J., and Lu, Z.L. (2013). An integrated reweighting theory of perceptual learning. Proc. Natl. Acad. Sci. USA *110*, 13678–13683. https://doi.org/10.1073/pnas.1312552110.
56. Tartaglia, E.M., Bamert, L., Mast, F.W., and Herzog, M.H. (2009). Human Perceptual Learning by Mental Imagery. Curr. Biol. *19*, 2081–2085. https://doi.org/10.1016/j.cub.2009.10.060.
57. Wang, R., Zhu, J., Rastan, S., Haghighat, F., and Yu, C. (2011). Perceptual learning transfers to untrained retinal locations after double training: A piggyback effect. J. Vis. *192*, 1026–1032. https://doi.org/10.1167/11.11.1026.
58. Bönstrup, M., Iturrate, I., Hebart, M.N., Censor, N., and Cohen, L.G. (2020). Mechanisms of offline motor learning at a microscale of seconds in large-scale crowdsourced data. NPJ Sci. Learn. *5*, 7. https://doi.org/10.1038/s41539-020-0066-9.
59. Shibata, K., Sagi, D., and Watanabe, T. (2014). Two-stage model in perceptual learning: toward a unified theory. Ann. N. Y. Acad. Sci. *1316*, 18–28. https://doi.org/10.1038/jid.2014.371.
60. Aberg, K.C., and Herzog, M.H. (2010). Does perceptual learning suffer from retrograde interference? PLoS One *5*, e14161. https://doi.org/10.1371/journal.pone.0014161.
61. Hung, S., and Seitz, A.R. (2011). Retrograde Interference in Perceptual Learning of a Peripheral Hyperacuity Task. PLoS One *6*. https://doi.org/10.1371/journal.pone.0024556.
62. Yotsumoto, Y., Chang, L.H., Watanabe, T., and Sasaki, Y. (2009). Interference and feature specificity in visual perceptual learning. Vis. Res. *49*, 2611–2623. https://doi.org/10.1016/j.visres.2009.08.001.
63. Censor, N., and Sagi, D. (2009). Explaining training induced performance increments and decrements within a unified framework of perceptual learning. Learn Percept *1*, 3–17. https://doi.org/10.1556/lp.1.2009.1.2.
64. Robertson, E.M., Pascual-Leone, A., and Miall, R.C. (2004). Current concepts in procedural consolidation. Nat. Rev. Neurosci. *5*, 576–582. https://doi.org/10.1073/pnas.95.23.13988.
65. Seitz, A.R., Yamagishi, N., Werner, B., Goda, N., Kawato, M., and Watanabe, T. (2005). Task-specific disruption of perceptual learning. Proc. Natl. Acad. Sci. USA *102*, 14895–14900. https://doi.org/10.1073/pnas.0505765102.
66. Kim, Y.H., Kang, D.W., Kim, D., Kim, H.J., Sasaki, Y., and Watanabe, T. (2015). Real-Time Strategy Video Game Experience and Visual Perceptual Learning. J. Neurosci. *35*, 10485–10492. https://doi.org/10.1523/JNEUROSCI.3340-14.2015.
67. Censor, N., Karni, A., and Sagi, D. (2006). A link between perceptual learning, adaptation and sleep. Vis. Res. *46*, 4071–4074. https://doi.org/10.1016/j.visres.2006.07.022.

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Software and algorithms		
MATLAB	MathWorks	https://www.mathworks.com/
SPSS Statistics 26	IBM	https://www.ibm.com/analytics/us/en/technology/spss

RESOURCE AVAILABILITY

Lead contact

Further information and requests should be directed to and will be fulfilled by the lead contact, Nitzan Censor (censornitzan@tauex.tau.ac.il).

Materials availability

This study did not generate new unique reagents.

Data and code availability

Data reported in this paper and any additional information for their analysis will be shared by the lead contact upon request.
This paper does not report original code.
Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Sixty-two healthy adults aged 18-40 years (12 males, average age 24.6 years SD = 3.5), participated in the study, which was conducted in accordance with a protocol approved by Tel Aviv University's Ethics Committees. All Participants provided written informed consent to participate in the study, had normal or corrected-to-normal vision, were not video gamers,[66] did not participate in other visual experiments during the study, and reported at least 6 h of sleep the night before each experimental session (performed during daytime).

One participant from the same-session performance group and two from the different-session performance group were not able to maintain stable performance at the fixation task due to fixation or dual-tasking instability and were excluded from the study. One participant from the same-session performance group was not included in the analysis due to an extreme long-term improvement score at location B (z-score < -4).

METHOD DETAILS

Stimuli and task

The standard texture discrimination task (TDT[1]), with a 10ms target screen, followed by a 100ms mask was used (Figure 1A). Observers had to discriminate whether a target array consisting of three diagonal bars (appearing 5.46º from the center of the visual field, either in the lower right (LR) or the upper left (UL) quadrant) was horizontal or vertical, and responded by pressing one of the two mouse buttons. The target stimulus was embedded in a background consisting of horizontal bars (19x19 bars, 0.57ºx0.04º spaced 0.86º apart, 0.04º jitter). Fixation was enforced by a forced-choice letter discrimination task, in which observers had to discriminate whether a rotated letter, presented in the center of the screen, was a T or an L, with auditory feedback for incorrect discrimination. Participants who demonstrated a lower percentage of correct choices in the fixation task compared to the peripheral task across all trials at a specific location were excluded from further participation in the study. Of note, this may indicate instability in either fixation itself or the ability to perform a dual task. Display size was $15.4° \times 15.1°$, viewed from 108 cm on a 20-in (50.8-cm) CRT HP p1230 monitor, refresh rate 100 Hz, mean texture luminance 84 cd/m^2. The time interval between the target stimulus and the mask (stimulus-to-mask onset asynchrony, SOA, measured from the onset of the target to the onset of the mask) ranged from 40 ms to 340 ms (40, 60, 80, 100, 120, 140, 160, 180, 200, 220, 240, 260, 300, and 340 ms) and was pseudo-randomized across trials. Each block consisted of 2 trials per SOA (for a total of 252 trials over nine blocks). To familiarize the participants with the task, pre-training blocks consisting of 10 trials were conducted prior to the first performance in each retinotopic location. These blocks were conducted initially with an SOA of 500 ms and then repeated with an SOA of 340 ms until subjects achieved 90% accuracy. A maximum of 10 blocks overall was provided, after which subjects who did not reach this criterion did not continue the experiment. Pre-training was followed by a short familiarization block of 1 trial per each SOA. To ensure reliable baseline measurements in both locations, participants were required to reach above 80% correct responses on the 3 highest SOAs and above 0.8 finger errors. All sessions were performed in a dark, quiet room.

Experimental design

In the first stage of the experiment, participants completed nine TDT (Figure 1A) blocks with the target stimulus presented in retinotopic location A (either UL or LR, condition A), followed by nine blocks performed in a different retinotopic location B (LR or UL, respectively, condition B; Figure 1B). The conditions were conducted either within the same session (same-session performance, n=29), or with an interval of ~48h between them (different-session performance, n=29). In the second stage of the experiment, long-term learning and generalization were measured in both same-session and different-session performance groups. Long-term learning was measured at location B following ~10 days (mean intervals and SE of 9.45$\pm$1.48 days for the same-session group, and 9.52$\pm$0.92 days for the different-session group), and long-term generalization effects were measured at location A immediately after location B in the same-session performance group and following ~48h in the different-session performance group.

QUANTIFICATION AND STATISTICAL ANALYSIS

The individual visual thresholds were calculated for each location performance using the standard Weibull fit for the psychometric curve with slope β and finger-error parameter 1-*p* yielding the function:[67]

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

Where *t* is the SOA, *P* is the success ratio (in the closed interval [0,1]) of target discrimination for a given SOA, and T is the threshold for each curve, defined as the SOA for which 81.6% of responses were correct when p=1.

Learning between locations A and B in the first stage of the experiment (and locations B and A in the second stage) was evaluated using repeated-measures analysis of variance (ANOVA), comparing the discrimination thresholds between locations. The experimental group was included as a between-subjects factor to assess the difference in learning magnitude between groups, and the identity of the retinotopic locations (LR_UL or UL_LR) was included as a covariate.

Long-term improvement within the same location was calculated for each participant as percent improvement from the first to the second stage of the experiment ((($threshold_{1^{st}\_stage} - threshold_{2^{nd}\_stage}$)/ $threshold_{1^{st}\_stage}$)*100). The magnitude of the long-term improvement was evaluated using one-sample t-tests across all participants. Then, to compare the difference in learning amplitude between groups, one-way ANOVA with the experimental group as a fixed factor was conducted. The initial thresholds and the identity of the retinotopic locations (UL or LR) were included as covariates.

To evaluate the relation between learning amplitude at locations A and B within each group, one-tailed Pearson's r coefficients were calculated.