BRIEF COMMUNICATIONS

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Memory reactivation improves visual perception

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Human perception thresholds can improve through learning. Here we report findings challenging the fundamental 'practice makes perfect' basis of procedural learning theory, showing that brief reactivations of encoded visual memories are sufficient to improve perceptual discrimination thresholds. Learning was comparable to standard practice-induced learning and was not due to short training *per se*, nor to an epiphenomenon of primed retrieval enhancement. The results demonstrate that basic perceptual functions can be substantially improved by memory reactivation, supporting a new account of perceptual learning dynamics.

Improvements in adult perceptual sensitivity have been observed across species and sensory domains. Notably, these effects have been documented to occur well beyond the critical period of development. Such improved perception has been attributed to brain plasticity mechanisms arising from repeated practice with the sensory stimulus[1,2]. Implicating a wide range of research disciplines extending from basic neurobiology to cognitive neuroscience, neurorehabilitation, and daily life activities, the prevailing and dominating dogma has been that 'practice makes perfect'[1,2]. Indeed, it is conceivable that, to induce such changes in neurobehavioral pathways that ultimately affect basic perception, repetitive-use-dependent plasticity mechanisms would be required. Such robust effects have been widely documented in visual, auditory, and olfactory modalities[1–4].

Here we provide evidence that brief reactivations of encoded visual memories by a reminder are sufficient to improve perceptual discrimination thresholds, similarly to learning achieved with standard repeated training. This challenges the fundamental practice-makes-perfect basis of procedural learning and memory theory. Our experimental design was based on a reactivation-reconsolidation framework stemming from consolidation research at the synaptic level. This framework has gained increasing experimental support, predominantly based on fear-conditioning models in rodents[5,6]. Notably, evidence has been accumulating for similar mechanisms in humans[7–9]. According to this notion, memories are dynamic even after their initial stabilization through consolidation. Thus, once an already consolidated existing memory is retrieved or reactivated by a reminder, it becomes susceptible to modification and can be degraded or strengthened. Motivated by these findings, we incorporated procedural reactivation–reconsolidation cycles into basic visual perception, classically referring to simple visual stimuli, lines, and textures, which are thought to be encoded in sensory brain regions or their higher-order readout pathways[2].

Human subjects performed a well-characterized visual discrimination task in which they determined the orientation of a target array of bars (**Fig. 1a**). The memory was first encoded and consolidated on a Day 1 standard session (252 trials; Online Methods), during which the discrimination threshold was measured. Participants then returned for three daily sessions, during which the encoded memory was reactivated with only five near-threshold reminder trials (memory-reactivation group), as in procedural memory reactivation, in which the originally encoded and consolidated trials constitute a reminder for memory reactivation[2,8,9]. An additional group of subjects performed full standard daily sessions (full practice group). A standard retest session was performed on Day 5 to measure the final discrimination thresholds (**Fig. 1b**).

Brief memory reactivations resulted in significant learning, which was also evident following the full standard practice, indicating that brief reactivations are sufficient to improve perceptual discrimination thresholds (**Fig. 1c**). In addition, we found no significant difference between total learning in the memory-reactivation group versus the full practice group (**Fig. 1c**). To further examine equivalence, we applied a Bayesian approach to confirm the lack of difference between effects[10–12]. The Bayes factor of comparing total learning across the two conditions (**Fig. 1c**) supported the claim of a genuine absence of effect[10]. Of note, this was additionally confirmed with the long-term experiments (see below). Moreover, learning in the memory-reactivation group was significantly greater than in the group that performed two-session learning without reactivation (Day 1 to Day 2 in full-practice conditions; **Fig. 1e**), further indicating that learning benefited from procedural memory reactivation. Thus, the results, supported by single-subject data (**Fig. 1d**), indicate that memory reactivation improves discrimination thresholds.

In light of the above results, we conducted a follow-up experiment in which we tested whether test–retest threshold differences with reactivation trials far from threshold are superior to a control condition measuring test–retest differences spaced days apart but without reactivations, as well as whether this learning is specific to the visual spatial location. Subjects performed the task with the reactivations trials far from threshold (target-to-mask asynchrony = 340 ms) or without reactivations between test and retest. The results show that test–retest differences with far-threshold reactivations were superior to test–retest without reactivations (**Fig. 1f**). This far-threshold, reactivation-induced learning (19.7% ± 4.6%), similar in magnitude to the near-threshold reactivation shown above (20.6% ± 5.5%), further supports a reactivation mechanism improving discrimination thresholds. Finally, the results showed that reactivation-induced learning was specific to the visual spatial location (with a new upper-left quadrant visual location similar to the test baseline threshold, 4.7 ± 8.4 ms

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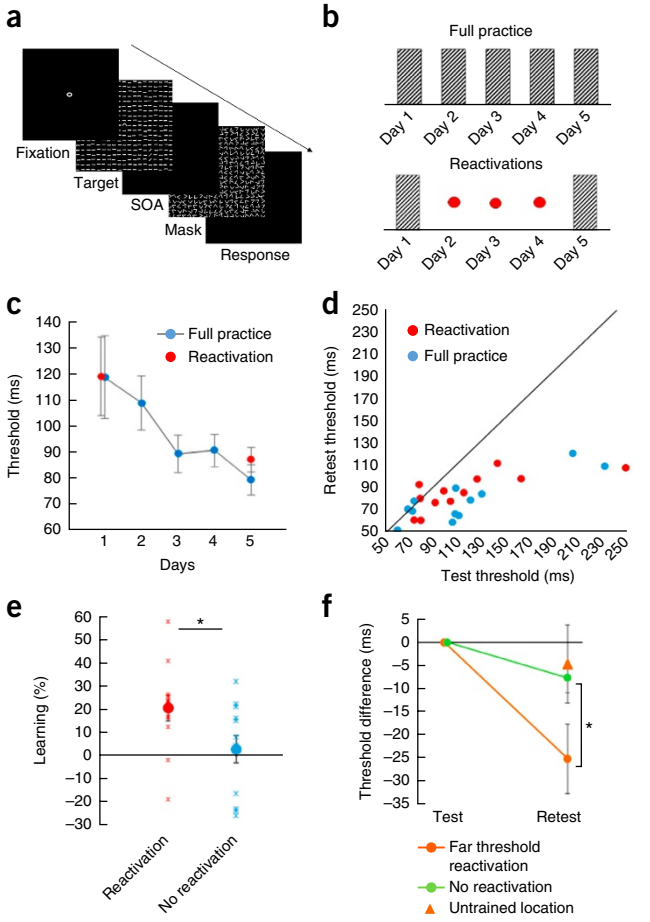

Figure 1 Improved discrimination thresholds following procedural memory reactivation. (**a**) Adult human observers were required to discriminate between horizontal or vertical orientations of a peripheral target consisting of three diagonal bars surrounded by horizontal lines. The target-to-mask asynchrony (SOA, measured from the onset of the target to the onset of the mask) was varied within the session to obtain a psychometric curve, from which the SOA discrimination threshold was derived. (**b**) A standard repeated-training condition consisted of five full consecutive daily sessions (252 trials per session; Online Methods). In the reactivation-reminder design, following encoding and consolidation of an initial session on Day 1, three daily reactivation episodes consisting of only five near-threshold trials were administered. A standard retest session was performed on Day 5 to measure final discrimination thresholds. (**c**) Learning curves in reactivation and repeated full standard practice conditions. Brief reactivations result in improved visual discrimination thresholds (mean Day 1 to Day 5 learning of 32.0 ± 12.2 ms, $F_{1,11} = 6.91$, $P = 0.023$; repeated measures ANOVA; $n = 12$). The induced learning was comparable to learning achieved with standard repeated-practice sessions ($n = 12$; 39.5 ± 11.4, $F_{1,11} = 11.94$, $P = 0.005$), with no significant difference between total learning in the memory reactivation (20.6% ± 5.5%) and in the full practice (26.6% ± 5.9%) groups ($F_{1,22} = 0.56$, $P = 0.46$; Bayes factor 0.47 ± 0.02)[10–12]. (**d**) Retest (Day 5) vs. test (Day 1) comparisons presented in a scatterplot along a unit slope line ($x = y$), in which each point reflects a participant. If data accumulate under the line, then thresholds are lower (better) at retest, indicating learning. (**e**) Improvements following memory reactivation were noticeably greater ($F_{1,22} = 4.87$, $^*P = 0.038$) than those following two-session learning without memory reactivation (Day 1 to Day 2 full practice group, 2.9% ± 5.8%). (**f**) Test–retest differences following far-threshold reactivations (25.1 ± 7.5ms) were superior ($n = 19$; $t_{15} = 2.13$, $^*P = 0.025$; Student's t test) to those achieved in a control condition measuring test–retest differences spaced days apart but without reactivations (7.6 ± 3.3 ms), and learning was specific to the visual spatial location. $^*P < 0.05$; error bars are s.e.m.

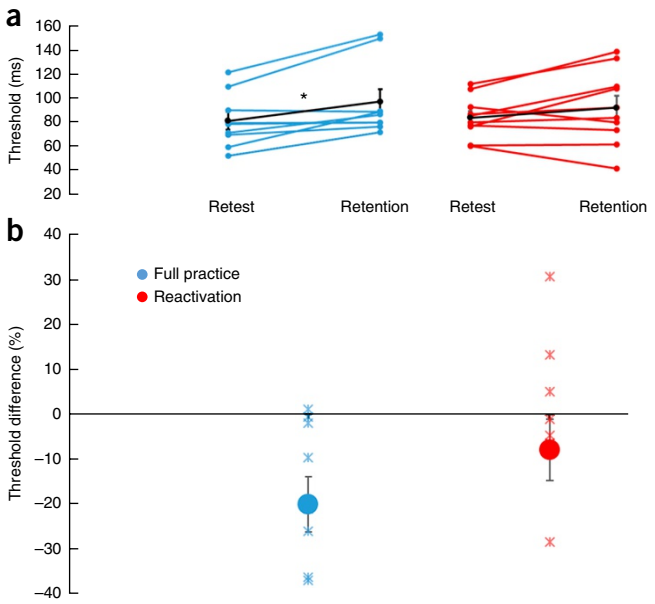

Figure 2 Long-term retention. (**a**) Individual thresholds at retest and at the long-term retention performance test conducted months later (see main text). Average thresholds marked in black lines. We found a significant deterioration in perception thresholds months following full standard practice (–15.8 ± 5.0 ms, $F_{1,8} = 9.91$, $^*P = 0.014$) that was not present in the reactivation group (–8.3 ± 5.7 ms, $F_{1,9} = 2.13$, $P = 0.18$). (**b**) Although overall retention was inferior in the full practice group, repeated-measures ANOVA showed that differences between retest and long-term retention performance following reactivation-induced learning (–7.9% ± 6.8%) were comparable ($F_{1,17} = 1.70$, $P = 0.21$) to full standard practice (–20.0% ± 6.1%).
$^*P < 0.05$; error bars are s.e.m.

difference; **Fig. 1f**), as has been widely shown in several forms of perceptual learning[1,2]. An additional, third replication of reactivation-induced learning was evident also in passive exposure conditions (unpublished data).

In light of the results showing that the induced learning was comparable to learning achieved with full standard practice, we sought to determine whether performance would also be comparable to standard practice over the long term. Therefore, participants from the original experiment returned for a test several months after the Day 5 retest (5.7 ± 0.4 months in the near-threshold reactivation group, 5.7 ± 0.5 months in the full practice group, $P = 0.99$). Notably, we observed a significant deterioration in perception thresholds months after the full standard practice that was not present in the reactivation group (**Fig. 2a**,**b**). However, although we noted that overall retention was inferior in the full practice group, it did not significantly differ between reactivation and full practice conditions (**Fig. 2b**). Long-term performance was also comparable across groups ($F_{1,17} = 0.19$, $P = 0.67$) when compared to their Day 1 baselines (reactivation, $F_{1,9} = 2.83$, $P = 0.13$; full practice, $F_{1,8} = 3.16$, $P = 0.11$). In sum, these results show that long-term performance following reactivation-induced learning was also comparable to full standard practice.

Could the observed reduction in perceptual thresholds result from enhanced primed performance *per se*, triggered by reactivations? To test this possibility, we had participants encode the memory on a Day 1 standard session and perform the three reactivation sessions on the retest day before the final discrimination threshold measurement (**Fig. 3a** and Online Methods). Reactivations did not enhance Day 1 to

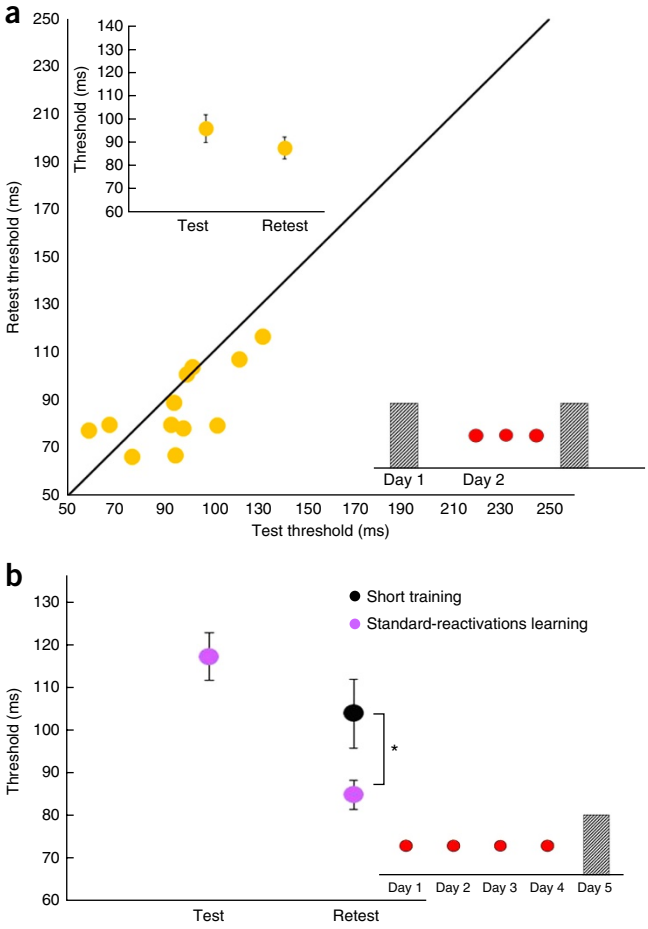

Figure 3 Improvements not explained by primed enhanced retrieval or short training *per se*. (**a**) ANOVA showed that, when reactivations were performed on the retest day before the final discrimination threshold measurement, learning ($n = 12$; Day 1 to Day 2, 6.6% ± 5.2%, top inset) was not enhanced compared to learning by the full practice group (Day 1 to Day 2, 2.9% ± 5.8%; $F_{1,22} = 0.22$, $P = 0.64$). (**b**) Final retest thresholds following short daily sessions ($n = 12$; 103.9 ± 8.0 ms) were higher than retest thresholds following standard and reactivations learning (85.0 ± 3.4 ms; ANOVA, $F_{1,46} = 6.32$, $^*P = 0.016$). Bottom insets show experimental designs; red dots indicate five trials each, as in the reactivations. $^*P < 0.05$; error bars are s.e.m.

Day 2 learning (**Fig. 3a**) compared to the full practice group. Overall, learning in these groups (4.7% ± 3.8%) was significantly smaller than the original daily brief reactivations group (20.6% ± 5.5%; $F_{1,34} = 5.65$, $P = 0.023$). These results indicate that reactivation-induced learning is not an epiphenomenon of primed retrieval enhancement and requires offline stabilization periods.

Could the short training (with only several trials) itself result in reduced perceptual thresholds, with or without a procedural memory reactivation mechanism? To address this question, we had participants perform only five trials each day, a procedure similar to the one used in the memory-reactivation condition; however, in this condition memory was not encoded with a full standard session on Day 1 (**Fig. 3b**). Discrimination thresholds following 4 d of such short training were significantly higher than retest thresholds following standard and reactivations learning (**Fig. 3b**). This further strengthens the notion that the improved perceptual thresholds were due to a memory reactivation mechanism rather than short training *per se*.

Taken together, the results here suggest that brief reactivations of consolidated perceptual memories may enable efficient perceptual learning, possibly via reactivation–reconsolidation cycles of memory strengthening[6,13] (without using interference interventions or competing tasks[7]). Thus, brief reactivations of the memory suffice for learning, whereas repetitive exposure may be redundant with no additive contribution to the learning process. Furthermore, the results show that reactivation-induced learning was not a manifestation of immediately primed enhanced retrieval and was therefore possibly mediated by sensory plasticity or functional interactions between early visual areas and higher-order brain regions[2], which should be further investigated in future studies.

Notably, short training *per se*, with only several trials, did not result in reduced perceptual thresholds. This is consistent with previous observations showing that, although in some tasks perceptual learning may benefit from shorter task exposure[14], prominent between-session learning in such tasks cannot be achieved below a minimal number of trials[15] and that even when learning occurs, it is far from being comparable to the learning achieved by full practice[15,16]. A possible explanation as to why attempts to reduce the amount of training in such tasks to only several trials have not been successful is that the encoding phase during the initial session needs to be comprehensive and intact for efficient initial consolidation to occur. Then, while initial encoding and consolidation are intact, as performed here, brief reactivations may trigger reconsolidation-like processes, strengthening the existing consolidated memory trace. It remains to be determined how such mechanisms may relate to priming-like single-exposure effects in perception[17] (as well as to the effects of imagery on learning[18]) and to spaced learning in other memory modalities[19] (although spaced learning, similarly to the control experiments here, may not result in prominent improvement in perceptual thresholds with only five trials, if it occurs independently of a reactivation–reconsolidation account, which here, even at suprathreshold conditions, enabled extensive learning). In addition, although spontaneous two-session test–retest differences[20] in our session structure and experimental design were substantially smaller than reactivation–induced learning, the relationship between these two forms of potential learning and their underlying neural mechanisms remains to be determined.

Of note, our results do not necessarily suggest that it is necessary to completely replace the practice-makes-perfect account stemming from mechanisms of use-dependent plasticity; rather they imply a more economic mechanism underlying improvement in visual perception. It remains to be determined whether similar mechanisms operate in other sensory modalities in perceptual learning or in cue-based reactivation mechanisms in other memory domains[5,6].

Our demonstration that basic perceptual functions can be improved by procedural memory reactivation supports a new account of perception and learning dynamics, enabled by using the memory-reactivation framework for perceptual learning research, challenges the practice-makes-perfect model as a unitary account in such forms of learning and has far-reaching clinical applications. These results may facilitate the development of strategies geared to substantially reduce the amount of practice needed for efficient learning in normal conditions and following neurological diseases or brain injuries.

METHODS

Methods, including statements of data availability and any associated references, are available in the online version of the paper.

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AUTHOR CONTRIBUTIONS

R.A.H., R.L.M., S.N., and N.C. designed the experiments. R.A.H., R.L.M., S.N., and N.C. collected the data. R.A.H., R.L.M., S.N., J.D.R., and N.C. analyzed the data. R.A.H., R.L.M., J.D.R., and N.C. wrote the paper.

COMPETING FINANCIAL INTERESTS

The authors declare no competing financial interests.

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ONLINE METHODS

Subjects. Seventy naive healthy subjects, ages 18–40 years (28 males, 42 females; mean age 24.5 ± 2.5 s.d.) gave their informed written consent to participate in the project, which was approved by Tel Aviv University's Ethics committee. All procedures were in accordance with approved guidelines. Customary sample sizes for psychophysical measurements were used, with each subject yielding large amounts of temporal data for perceptual threshold analyses. No statistical methods were used to predetermine sample sizes, but our sample sizes are similar to those generally employed in the field. Subjects were randomly assigned to the experiments, which were conducted in a single-blinded fashion. All participants had normal or corrected-to-normal vision, were not video gamers, did not participate in other visual experiments between spaced sessions of test and retest, and reported at least 6 h of sleep the night before each experimental session (performed during daytime). Three subjects were excluded due to repeated fixation and mistyping errors, which prevented reliable measurement of the peripheral discrimination threshold, and when their performances were flagged by SPSS as outliers based on a comparison to the interquartile ranges of all subjects.

Stimuli and task. Participants performed a standard texture discrimination task (TDT)[1], with a target frame (10 ms) followed by a patterned mask (100 ms; **Fig. 1a**). 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 5.72°) was horizontal or vertical. The target was embedded in a background of horizontal bars (19 × 19, 0.57° × 0.04° and spaced 0.86° 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 an auditory feedback. Display size was 15.4° × 15.1° (viewed from 100 cm away on a 20-in (50.8-cm) CRT HP p1230 monitor, refresh rate 100 Hz, mean texture luminance 84 cd/m^2).

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 session consisted of 18 trials per SOA (total of 252 trials).

To familiarize the subjects with the task, a pretraining block of 10 trials at 340 ms SOA was conducted before the first session[14]. This block was repeated until subjects reached 90% correct responses (a maximum of 10 blocks, after which subjects who did not reach the criterion were excluded from the experiment). Pretraining was followed by a short familiarization block of 1 trial per each SOA.

Experimental design. The memory was first encoded and consolidated on a Day 1 standard session (252 trials; see above), in which the discrimination threshold was measured. Participants then returned for three daily sessions, in which the encoded memory was reactivated with only five near-threshold trials. Reactivation trials were set individually at the SOA given in the initial session that was closest to threshold. A standard retest session (252 trials) was performed on Day 5 to measure the final discrimination thresholds (reactivation group, n = 12, ages 25.0 ± 3.5 years; **Fig. 1b**). An additional group of subjects performed full standard daily sessions (252 trials per session, full practice group, n = 12, 24.5 ± 2.2 years; **Fig. 1b**). Both groups returned for an additional standard session in which long-term performance was measured (reactivation, n = 10, mean 5.7 ± 0.4 months after retest; full practice, n = 9, 5.7 ± 0.5 months; no differences in time interval, P = 0.99; **Fig. 2**).

A similar follow-up experiment tested whether learning with reactivation trials far from threshold is superior to a control condition measuring test–retest learning spaced days apart but without reactivations and whether this learning is specific to the visual spatial location. Participants (n = 19, 24.9 ± 2.0 years) performed the task with reactivations trials far from threshold or with no reactivations at all between test and retest (n = 12 at SOA = 340 ms and n = 7 with no reactivations). Retest was conducted 9 d after the encoding session, and the three reactivations were conducted every 2–3 d. To test whether reactivation-induced learning was specific to the visual spatial location[2], following the final retest, participants (reactivation, n = 12) also performed a standard threshold measurement in a new visual location (similar target stimulus but at the upper left quadrant of the visual field, at 5.72°; **Fig. 1f**).

To test whether the observed reduction in perceptual thresholds result from primed enhanced performance *per se*, triggered by reactivations, we had participants (n = 12, aged 23.8 ± 2.2 years) encode the memory on a Day 1 standard session and perform the three-reactivation session on the retest day, Day 2, before the final discrimination threshold measurement (**Fig. 3a**).

To test whether short training *per se* with only a small number of trials resulted in reduced perceptual thresholds, regardless of memory reactivation mechanism, we had participants (n = 12, aged 23.9 ± 2.4 years) perform only five trials each day, as in the memory reactivation condition; however, in this condition memory was not encoded with a full standard session on Day 1. Thus, they performed four daily consecutive short training sessions followed by a standard session on Day 5 (**Fig. 3b**).

Data and statistical analysis. A daily threshold was calculated for each session using the standard Weibull fit for the psychometric curve, with slope β and finger-error (mistyping) parameter $1 - p$, yielding the function[14]

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

where T is the threshold for each curve, defined as the SOA for which 81.6% of responses were correct when P = 1. No blinding was employed during data analysis.

Repeated-measures ANOVA were conducted to evaluate learning in each group by comparing standard initial test thresholds and final retest thresholds. One-way ANOVA was used to compare learning percentages between groups, with a hypothesis-driven planned comparison t test for the follow-up experiment. Data distribution was assumed to be normal, but this was not formally tested. Standard error-rates of 0.05 were used, using confirmatory analyses required in additional follow-up experiments secondary to the main findings.

Data availability. The data that support the findings of this study are available from the corresponding author upon reasonable request. A **Life Sciences Reporting Summary** is available.

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Corresponding author(s): Nitzan Censor

☐ Initial submission ☐ Revised version ☒ Final submission

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Experimental design

1. Sample size

Describe how sample size was determined.

Customary sample sizes for psychophysical measurements were used, with each subject yielding large amounts of rich temporal data for perceptual threshold analyses. No statistical methods were used to pre-determine sample size but our sample sizes are similar to those generally employed in the field.

2. Data exclusions

Describe any data exclusions.

All participants had normal or corrected-to-normal vision, were not video gamers, nor participated in other visual experiments between spaced sessions of test and retest, and reported at least 6 hours of sleep the night before each experimental session. Three subjects were excluded due to repeated fixation and finger errors, which do not allow a reliable measurement of the peripheral discrimination threshold, and as interquartile range-based flagged observations generated by SPSS.

3. Replication

Describe whether the experimental findings were reliably reproduced.

An additional experiment yielded similar reactivation-induced learning even in far-threshold conditions (Fig. 2d).

4. Randomization

Describe how samples/organisms/participants were allocated into experimental groups.

Subjects were randomly assigned to the experiments.

5. Blinding

Describe whether the investigators were blinded to group allocation during data collection and/or analysis.

Experiments were single blinded. No blinding was employed during data analysis.

Note: all studies involving animals and/or human research participants must disclose whether blinding and randomization were used.

6. Statistical parameters

For all figures and tables that use statistical methods, confirm that the following items are present in relevant figure legends (or in the Methods section if additional space is needed).

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☐	☒ The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement (animals, litters, cultures, etc.)
☐	☒ A description of how samples were collected, noting whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☐	☒ A statement indicating how many times each experiment was replicated
☐	☒ The statistical test(s) used and whether they are one- or two-sided (note: only common tests should be described solely by name; more complex techniques should be described in the Methods section)
☐	☒ A description of any assumptions or corrections, such as an adjustment for multiple comparisons
☐	☒ The test results (e.g. *P* values) given as exact values whenever possible and with confidence intervals noted
☐	☒ A clear description of statistics including central tendency (e.g. median, mean) and variation (e.g. standard deviation, interquartile range)
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7. Software

Describe the software used to analyze the data in this study.	Matlab, SPSS, R

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Materials and reagents

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8. Materials availability

Indicate whether there are restrictions on availability of unique materials or if these materials are only available for distribution by a for-profit company.	No unique materials were used.

9. Antibodies

Describe the antibodies used and how they were validated for use in the system under study (i.e. assay and species).	No antibodies were used.

10. Eukaryotic cell lines

a. State the source of each eukaryotic cell line used.	No eukaryotic cell lines were used.
b. Describe the method of cell line authentication used.	No eukaryotic cell lines were used.
c. Report whether the cell lines were tested for mycoplasma contamination.	No eukaryotic cell lines were used.
d. If any of the cell lines used are listed in the database of commonly misidentified cell lines maintained by ICLAC, provide a scientific rationale for their use.	No commonly misidentified cell lines were used.

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11. Description of research animals

Provide details on animals and/or animal-derived materials used in the study.	No animals were used.

Policy information about studies involving human research participants

12. Description of human research participants

Describe the covariate-relevant population characteristics of the human research participants.	70 naïve healthy subjects, ages 18-40 years (28 males, 42 females, mean age 24.5 ±2.5 s.d.).