This version of the manuscript has been accepted for publication. The original article can be found under
<https://doi.org/10.1007/s41465-019-00121-y>

Cite as:

Ovalle Fresa, R., & Rothen, N. (2019). Training enhances fidelity of color representations in visual long-term memory. *Journal of cognitive enhancement*, 3(3), 315-327. <https://doi.org/10.1007/s41465-019-00121-y>

Training enhances fidelity of color representations in visual long-term memory

Rebecca Ovalle Fresa and Nicolas Rothen

Institute of Psychology,

University of Bern, Bern, Switzerland

and

Department of Psychology,

Swiss Distance Learning University, Brig, Switzerland

Author Note

Correspondence concerning this article should be addressed to Rebecca Ovalle Fresa, University of Bern, Institute of Psychology, Fabrikstrasse 8, 3012 Bern, Switzerland. E-mail: rebecca.ovallefresa@gmail.com

This work was supported by the Swiss National Science Foundation (Grant Number: PZ00P1_154954).

Abstract

Visual perception can be affected by training mental representations. However, it remains unclear if training procedures can also affect the quality of mental representations. To investigate if training enhances the fidelity of mental representations retrieved from visual long-term memory (VLTm), we used a task including object-color associations with a continuous response-space. We tested 15 participants in a training group, and 15 participants in a control group. Training consisted of six training runs executed on three consecutive days. Before and after training, we assessed accessibility and fidelity of mental representations in VLTm, and of single objects in visual short-term memory (VSTM). Not only accessibility to mental representation but also their fidelity increased across training and transferred to novel object-color associations in VLTm and VSTM after training. At the end of the training, fidelity of VLTm representations were virtually identical to fidelity of VSTM representations. We conclude, that training object-color associations does not only improve the accessibility of VLTm representations, but also their fidelity based on perceptual plasticity of the visual system.

Keywords: perceptual plasticity, perceptual learning, visual memory, mnemonic precision

1. Introduction

In visual perception, internal representations are built while an object is being viewed. In visual mental imagery, such mental representations with experience of sensory information occur although no external stimulus is present (Kosslyn et al., 1993; Pearson, Naselaris, Holmes, & Kosslyn, 2015). These two mechanisms have a lot in common, as for example a shared neural basis in visual areas (e.g., Kosslyn et al., 1993, for a review see Pearson, Naselaris, Holmes, & Kosslyn, 2015). Due to the neural plasticity of the visual system, repeated practice can enhance discrimination or detection performance on visual tasks (Doshier & Lu, 2017; Watanabe & Sasaki, 2015). This process is termed perceptual learning and has been observed for example in single features as color (e.g., Özgen & Davies, 2002; Thurston & Dobkins, 2007), orientation (Doshier & Lu, 1998; Schoups, Vogels, & Orban, 1995; Schoups, Vogels, Qian, & Orban, 2001), spatial frequency (Bennett & Westheimer, 1991; Fiorentini & Berardi, 1980, 1981) or contrast (Fiorentini & Berardi, 1980, 1981). The underlying shared neural mechanisms of visual mental imagery and the perceptual system suggests that like perceptual learning, precision of mental representations might also be trainable. Perceptual learning is also observed when the training is rather based on mental imagery than on physical perception (Mast, Tartaglia, & Herzog, 2012; Tartaglia, Bamert, Mast, & Herzog, 2009). However, it seems to be more difficult to test if mental representations can be enhanced through training (Rademaker & Pearson, 2012). Therefore, the primary goal of our study was to investigate the impact of training on mental representations retrieved from visual memory. More precisely, we investigated if training can enhance the fidelity of visual mental color representations retrieved from visual long-term memory (VLTm).

Visual memory is used to encode, store, and retrieve mental representations of visual information. When a mental representation is maintained for a few seconds after presentation of a visual display, we will refer to this process as visual short-term memory (VSTM). For the purpose of present study, we were specifically interested in the sustained maintenance of a *single* item in VSTM. When visual information is encoded and stored in memory, and the representation is recalled after delays longer than a few minutes, we will refer to it as VLTm.

Different approaches exist to measure retrieval performance for mental representations in visual memory: common approaches differentiate between accessed and not accessed mental representations and quantify the number of retrieved representations from a preceding encoding phase (e.g., Baddeley & Hitch, 2017; Rajaram, 1996). Henceforth, quantitative measures are referred to as *accessibility* of mental representations. Other approaches are concerned with the quality of mental representations (e.g., Brady, Konkle, Gill, Oliva, & Alvarez, 2013; Konkle, Brady, Alvarez, & Oliva, 2010). Namely, with the question at which level of precision mental representations can be retrieved. We will refer to the qualitative aspect as *fidelity* of mental representations.

In order to compare the fidelity of color perception with the fidelity of mental color representations retrieved from VSTM and VLTm, Brady et al. (2013) combined the delayed estimation paradigm with object-color associations (e.g., Fougner, Suchow, & Alvarez, 2012; Prinzmetal, Amiri, Allen, & Edwards, 1998; van den Berg, Shin, Chou, George, & Ma, 2012; Wilken & Ma, 2004; Zhang & Luck, 2008). The use of color as a continuous response space had the advantage to assess subtle changes in the precision of

these representations. The same paradigm was used to assess perception, VSTM and VLTM, which allowed for a direct comparison of the precision for the different levels of mental representations. In the three tasks, the study objects were presented each in a different, randomly selected monochrome color, the original color. The same objects were also presented in grey, representing the response object. On a color wheel surrounding the response object, participants had to adjust its color to match the color of the study object. In the perceptual task, the study object and the response object were presented simultaneously on both sides of a central fixation cross. The study object in the original color was always visible and it was not required to rely on a mental representation. In the VSTM task, one, three, or five study objects were presented on one screen, the response object appeared after a delay of 1000 ms. Across this delay, a mental representation of the study object-color association had to be maintained. The VLTM task consisted of a study and a test phase. In the study phase, study objects were subsequently presented in distinct colors. Participants were instructed to encode the object-color associations. Response objects were presented in a recall phase immediately after the study phase. In this task, participants had to recall a mental representation of the original color (i.e., color of the specific object from the learning phase) for each object from VLTM. The deviation of the response color from the target color was assessed as the dependent variable. Applying a computational modelling approach (i.e., the standard mixture model) allowed to estimate the fidelity and the accessibility of the color representations. The results showed that fidelity was generally lower for VLTM representations than for VSTM representations. However, fidelity of VLTM

representations was comparable to fidelity of VSTM representations, when VSTM reached maximum capacity (namely in the condition with five presented objects).

Since this study, only few studies investigated the impact of manipulations on the fidelity of VLTM representations. These results showed that on the one hand, precision for color representations in VLTM was enhanced through the induction of negative emotions (Xie & Zhang, 2017, 2018). In their first study, Xie and Zhang (2017a) found enhanced precision for VLTM representations when during study and during recall phase negative emotions (compared to neutral emotions) were induced. When study context and test context both were positive, precision of recall was comparable to the neutral condition. In their second study, the authors reported an increased precision of VLTM representations when the objects during study phase were preceded by negative associated pictures, compared to neutral and positively associated pictures (Xie & Zhang, 2017). On the other hand, precision of VLTM representations was not influenced by encoding strategies (Sutterer & Awh, 2016). Here, a retrieval practice condition, where after every 10 trials the colors had to be recalled, was compared to a restudy condition where the encoding trials were repeated, and to a control condition with no additional presentations. Results revealed no differences in precision of VLTM representations between the three conditions. Together, the results of these studies can be interpreted that the fidelity of mental representations retrieved from VLTM seems to be enhanced by negative emotions, but insusceptible to encoding strategies.

Evidence from mental imagery studies suggests that perceptual learning also occurs when the training is based on mental imagery (Mast, Tartaglia, & Herzog, 2012; Tartaglia, Bamert, Mast, & Herzog, 2009). Tartaglia et al. (2009) demonstrated this using

a training with a vertical line bisection task. Participants were divided into two groups: the perceptual learning group and the mental imagery group. Participants in the perceptual learning condition were trained with stimuli consisting of three vertical lines. Their task was to decide if the middle line was closer to the left or to the right-outer line. Participants in the mental imagery conditions were presented with only the two outer lines and had to visualize the middle line either more on the left (indicated by a low-frequency tone) or more on the right (indicated by a high-frequency tone). Both trainings led to similar improvements for the trained vertical lines, with only a marginal stronger effect in the perceptual training condition. Interestingly, a transfer of the benefit to untrained horizontal lines was comparable for both training conditions. Control experiments without training revealed no improvement in line bisection between two sessions. The results suggest that repeated creation of mental representations leads to perceptual learning effects in a line bisection task and indicate that also mental representations can lead to neural changes in early visual areas.

By contrast, Rademaker & Pearson (2012) did not find enhanced mental representations after a mental imagery training with colored Gabor patches. In the training task, participants were cued to imagine either a green or a red Gabor patch for 8 s per trial. Strength of visual mental imagery was measured before and after training by means of binocular rivalry. This phenomenon describes the effect that when a different stimulus is presented to each eye, it is only possible to consciously perceive one of these stimuli at a time. Stimuli previously held in front of the mental eyes tend to be more often consciously perceived than new stimuli (e.g., Pearson, Clifford, & Tong, 2008; Rademaker & Pearson, 2012). In addition, subjective experience of imagery strength was

assessed on a trial-by-trial basis. Results showed an increasing relation between subjective experience and imagery strength across training, but no effect of training on imagery strength assessed by binocular rivalry. One possible explanation for this result is, that it is not possible to improve imagery strength by practice, possibly because imagery might not be powerful enough to induce plastic changes at low sensory levels. Another explanation might be found in the method to assess mental imagery strength. That is, the dichotomous measure of the used binocular rivalry task might not have been sensitive enough to detect subtle changes in the fidelity of mental imagery.

In a more recent study, the impact of working memory training on the fidelity of VSTM representations was investigated (Buschkuehl, Jaeggi, Mueller, Shah, & Jonides, 2017). Two groups were trained across ten days in one of two versions of a change detection task. In both task versions, four colored squares were presented simultaneously. Colors were selected from a palette of seven distinct colors. After a short delay the four squares appeared again, and participants had to decide if one of the squares had changed its color. In one group, the locations of the squares were masked during the delay, and all four squares were presented again. The square of interest was marked with a black circle. In the other group, only one square was presented after the delay without masking. Before and after the training, participants were tested with a delayed estimation task to assess the fidelity of VSTM representations for the colors used in the change detection task. During each trial, participants were briefly presented with three colored squares, followed by a short delay and a screen with three placeholders at the locations of the previously presented squares. The color of the marked placeholder had to be adjusted by means of a color wheel to match the color of the square that was presented at the same

location. Performance after training improved in the trained change detection task, but no enhancement in the fidelity of VSTM representations was found. Thus, benefits of a working memory training did not transfer to the fidelity of mental representations in a different task.

Summarizing, evidence exists that training mental imagery and the reactivation of visual memory representations can lead to perceptual learning (Amar-Halpert, Laor-Maayany, Nemni, Rosenblatt, & Censor, 2017; Mast et al., 2012; Tartaglia et al., 2009). Other studies showed that experimental manipulations can affect the fidelity of mental representations retrieved from VLTM (Xie & Zhang, 2017, 2018). By contrast, it seems to be more difficult to find an impact of training on the fidelity of mental representations (Buschkuehl et al., 2017; Rademaker & Pearson, 2012), maybe due to methodical reasons. For instance, Rademaker and Pearson used a binary response space and Buschkuehl et al. did not train the precise recall of a perceptual feature, but only its recognition.

Hence, it was our primary goal to test if training to precisely recalling a color in a continuous response space would not only enhance the accessibility of mental color representations from VLTM, but also their fidelity. Furthermore, we were interested, if the training effect transfers to novel stimuli and a different task (i.e., VSTM). We adapted the VLTM task introduced by Brady et al. (2013), using their perceptual task to encode object-color associations (study phase). The objects and randomly associated colors were presented from the same list in the session before the training (pre-training session) and in the six training runs, realized in three training sessions on three consecutive days. To assess transfer, different object-color associations were used in the session after training

(post-training session). Further, we assessed more distant transfer of benefits onto a VSTM task based on the same paradigm with a memory load of one item (i.e., sustained maintenance). In all tasks, we assessed overall task performance in terms of the deviation in degrees between the response and the target color. As this measure also includes mental representations not retrieved from memory (guesses), we applied a standard mixture model (Zhang & Luck, 2008) to estimate the amount of guessing and the fidelity of retrieved mental representations independently from each other. We expected an increase in performance over the course of the training. With regards to the estimated parameters, we expected a reduction in the number of guesses and an increase in the fidelity of the retrieved mental representations. Furthermore, we explored a potential transfer of benefits to novel object-color associations and the untrained VSTM task.

2. Method

2.1 Participants

Since there was no similar study to conduct a-priori power analyses, we decided for a practical approach. Sample-size determination was based on the study that introduced the delayed estimation task to investigate precision in VLTm (Brady et al., 2013). We took their largest sample ($N = 9$) and increased it by approximately 50%. That is, we aimed for 15 participants per condition.

Inclusion criteria were normal vision (or corrected to normal vision). We tested a convenience sample consisting of colleagues, friends and psychology students of the University of Bern, who earned course credits in return for study participation. We tested a total of 31 participants, whereby one participant had to be excluded due to a total error score of 18.9 in an online version of the Farnsworth Dichotomous Test, which was more

than 3 standard deviations above the group mean and interpreted to indicate color blindness (D-15; <http://www.color-blindness.com/color-arrangement-test/>; e.g., Vingrys & King-Smith, 1988). Fifteen participants were part of the training group and 15 of the control group. Participants in the training group had a mean age of 27.67 years ($SD = 7.15$ years, range: 20 – 45 years), 10 were female and all right handed. Participants in the control group had a mean age of 21.80 years ($SD = 2.60$ years, range: 19 – 27 years), 13 were female and one was left-handed. Although the training group was significantly older than the control group ($t(28) = 2.99, p = .006, d = 1.09$), they showed virtually identical average total error scores in the Farnsworth Dichotomous Test ($t(28) = 0.67, p = .510, d = 0.24$), which was 11.89 ($SD = 0.78$) in the training group and 11.71 ($SD = 0.70$) in the control group. The study was approved by the local ethics committee of the University of Bern. Participants were informed that they could withdraw at any time during the experiment before they consented to participate.

2.2 Apparatus and materials

Stimuli were rendered in MATLAB using Psychophysics Toolbox 3 (Brainard, 1997; Pelli, 1997) and were presented on a flat 21-inch Sony Trinitron cathode ray tube monitor (85 Hz refresh rate) driven by a NVIDIA GeForce GTX970 graphics card (NVIDIA Corporation, Santa Clara, California) with a spatial resolution of 1280×1024 pixels and a color resolution of 8 bits per channel. The CIE1931 chromaticity coordinates and luminance of the monitor primaries were $R = (0.625; 0.341; 18.061)$, $G = (0.287; 0.609; 52.860)$, and $B = (0.150; 0.073; 6.145)$. A chin- and forehead rest was used to keep the viewing distance of 100 cm constant for the duration of the experiment. A black cardboard tunnel led directly from the monitor to the chin- and forehead rest and

overlapped it by 20 cm at the top and both sides to shield peripheral vision and guarantee that the visual system of the participants adapted to the computer monitor.

2.2.1 Visual test and color-blindness test: We assessed participant's visual acuity with a printable version of the Landolt rings test (www.sov.ch; compare Wesemann, Schiefer, & Bach, 2010). To assess color vision, we applied an online version of the Farnsworth Dichotomous Test Farnsworth Dichotomous Test (D-15; www.color-blindness.com/color-arrangement-test; e.g., Vingrys & King-Smith, 1988).

2.2.2 Color memory tasks: Stimuli consisted of 185 distinct and identifiable objects from the Bank of Standardized Stimuli (Brodeur, Dionne-Dostie, Montreuil, & Lepage, 2010) which were randomly assigned to five lists of different objects: a practice list consisting of five objects and four testing lists consisting of 45 objects each. One-hundred-and-eighty colors were assigned to four lists. Colors represented every second degree on an isoluminant color circle. Colors in each of the four lists differed in steps of 16 degrees on the color circle. Each of the four lists was assigned to one of the stimulus lists, resulting in four different object-color lists. For the practice list, five colors were randomly chosen.

The original objects were converted to greyscale and adjusted to red (RGB = 125, 0, 0) in Irfanview (version: 4.42, © 2016 by Irfan Skiljan). During the experiment, stimuli were resized to $5^\circ \times 5^\circ$ of visual angle, converted to CIELUV color space, and greyscaled by means of adjusting chromaticity to zero and retaining lightness. Gamma corrections were applied based on the measured gamma curves of the monitor primaries. Next, the lightness of each object was compressed by setting the L^* of each pixel to 25% of its original value. Then, the objects were shifted along the L^* -axis that the averaged

luminance of the object was isoluminant with the background of the monitor. Thereafter, one of the different test colors which were equidistantly sampled along an isoluminant hue circle in CIELUV space ($L^* = 76$, $u^* = 0$, $v^* = 0$, radius of 28) was randomly assigned to each of the objects without replacement, resulting in *unique object-color associations for each participant*. Compression was necessary to make sure colors were rendered within the gamut of the monitor. Pixels with values > 98 on the L^* -axis were masked with the background color to remove untidy borderlines.

The luminance of the background was $y = 40.7 \text{ cd/m}^2$. The background was used as the white point for the conversion into CIELUV space. Hence the lightness of the background was $L^* = 76$. This definition of the white point avoids L^* -values above 100, when parts of the stimuli were lighter than the background (cf. Witzel & Franklin, 2014). For important implications of careful color rendering the reader is referred to the following research articles (Allred & Flombaum, 2014; Bae, Olkkonen, Allred, & Flombaum, 2015; Bae, Olkkonen, Allred, Wilson, & Flombaum, 2014).

2.3 Procedure

Figure 1a shows the study procedure. The training group started with a pre-training session on the first day, followed by six training runs with the VLTM task over the course of the next three days (two runs per training session), and a post-training session on the fifth day. In order to test if task repetition alone leads to performance enhancements, the control group attended the pre- and post-training sessions with an unfilled interval of three days. At the beginning of the pre-training session, we first assessed demographic data, tested visual acuity (Landolt ring test; www.sov.ch; compare

Wesemann, Schiefer, & Bach, 2010) and color blindness (Farnsworth Dichotomous Test (D-15); online on www.color-blindness.com/color-arrangement-test).

Figure 1. A) Training procedure with the task order per session. The pre-training and post-training sessions, and the three training sessions took place on five consecutive days. B) Trial procedure of the VSTM task. C) Trial procedure for the study phase and D) the test phase of the VLTm task.

In the pre-training session, memory was tested with the VSTM task followed by the VLTM task. The order was reversed in the post-training session. The VLTM task consisted of a study phase, which can be described as perceptual color-matching task (Brady et al., 2013), and a recall phase. In all sessions, participants were individually tested in a completely darkened room and received the instruction to rest their chin and forehead on the respective parts of the chin- and forehead rest during the experiment. Color adaptation was guaranteed by presenting written instructions and five initial practice trials on the grey screen in each task.

The VSTM task started with five example trials followed by 45 experimental trials. There was only one condition with a memory load of one object. The procedure of one trial is shown in Figure 1b. It started with a fixation cross presented for 1000 ms, then the study object in the target color appeared for 3000 ms. After a delay with a central fixation cross of 1000 ms the same object reappeared in grey (the response object), surrounded by a black circle with a radius of 3.5° of visual angle. This black circle represented an underlying color wheel. Participants adjusted the color of the initially grey object to the target color by moving a black dot on the circle by means of the computer mouse. Upon the first mouse movement the grey object changed the color according to the underlying color wheel. By mouse-click, the color was chosen and the next trial was initiated. The starting point of the color wheel was randomized for each sample to avoid position effects. The focus lied on accuracy, response time was not restricted.

The VLTM task followed a similar procedure. The study phase started with five example trials and consisted of 45 experimental trials. The trial procedure is depicted in

Figure 1c. First, a fixation cross appeared for 1000 ms. Then, the study object and the grey-scaled response object appeared simultaneously on the screen on both sides of a central fixation cross. The study object was presented on the left and the response object on the right side. The distance from the central fixation to the center of each of the objects was 5° of visual angle. Each object was surrounded by a black circle, whereas only the circle of the response object was representing a color wheel. Participants adjusted the color of the response object to the target color by mouse. The mouse click initialized the next trial. Besides adjusting the color of the object on the right, participants were further required to memorize the color of each object.

In the VLTM test phase the objects from the study phase were presented again as grey-scaled response objects. It started with five example trials, followed by 45 experimental trials. The trial procedure is shown in Figure 1d. Each trial started with a central fixation cross for 1000 ms, followed by the presentation of the grey response object which was surrounded by the black circle. The fixation cross stayed on the screen with the grey object, until the first mouse-movement. Participants adjusted to color of each response object to the memorized target color from the study phase. By mouse click the chosen color was submitted and the next trial was initiated.

For each participant and task, object-color associations were randomly determined within a given object-color list. However, for a given participant, the specific object-color associations of the VLTM task during the pre-training session remained identical for all training runs. A different list of objects and colors was used for the VLTM task during the post-training session. The order of the lists was counterbalanced across the pre-training and post-training sessions. The remaining two lists were assigned to VSTM task

of the pre-training and post-training session, respectively. The assignment of the lists to the VSTM of the pre-training and post-training session task was counterbalanced. The assignment of the two lists to the VLTM and VSTM task, respectively, was counterbalanced between the two tasks, so that always the same two lists were associated with the VLTM task or the VSTM task.

3. Analysis

3.1 Overall performance (model-free approach)

Response errors, reflecting the deviation of the selected color from the target color, were measured in degrees and could lie between 0° (no deviation from a given color) and $\pm 180^\circ$ (maximal deviation from a given color). The first analysis was concerned with overall performance. For every participant, we calculated the median of their absolute response errors (the central tendency of the absolute response errors) per condition. We preferred the median over the mean to minimize the bias of potential outlier responses in datasets of individual participants (Leys, Ley, Klein, Bernard, & Licata, 2013), reducing the influence of outlier trials in which the responses reflect pure guesses.

3.2 Estimated parameters (standard-mixture model)

Because averaged central tendencies of performance (i.e., overall performance) in the VLTM and VSTM task are potentially confounded by guesses, we applied the standard mixture model of (Zhang & Luck, 2008) to our data to gain further insights about the fidelity of the stored mental representations. The model explains the distribution of the deviations from the target color as mixture of two distributions: the first, a von Mises distribution (comparable with a Gaussian distribution considering the

circular nature of the color wheel) centered on the target color, constituting the correct responses. The standard deviation (SD) of the von Mises distribution reflects precision with which the remembered colors were selected (with lower values reflecting higher performance). This parameter is interpreted as reflecting fidelity. The second, a uniform distribution defined by parameter g reflecting the proportion of guesses, interpreted as memory accessibility. Due to small trial numbers per condition, we aggregated trials across participants for a given condition (cf. Fan, Hutchinson, & Turk-Browne, 2016) and used the MemToolbox (Suchow, Brady, Fournie, & Alvarez, 2013) to estimate the parameters of the two distributions by fitting the response errors with a Markov Chain Monte Carlo (MCMC). This procedure resulted in Maximum a Posteriori (MAP) estimates for the parameters SD and g . In addition, a 95% Bayesian credible interval was calculated for each of the two parameters, from each parameter's distribution created in the MCMC sampling procedure. Credible intervals can be used to derive statistical decision. Conditions with non-overlapping 95% Bayesian credible intervals are commonly interpreted as significantly different from each other (cf. Sutterer & Awh, 2016).

Furthermore, we assessed the reliability of the parameter estimates using a bootstrapping approach, because aggregation of trials across participants does not consider between-subject variability (cf. Fan, Hutchinson, & Turk-Browne, 2016). The idea behind this method is that the model estimates on subsets of the observations on a given iteration should reveal similar results as the model estimated across participants to the extent that, the effect of our parameter estimates across participants was reliable. Thus, we randomly sampled 45 data points with replacement from all data points of one

condition for each of 15 simulated participants. This procedure was repeated in 500 iterations for each condition separately, resulting in 500 new model fits per condition.

4. Results

4.1 Overall performance

4.1.1 VLTm study. Descriptive statistics for the study phase of the VLTm task are listed in Table 1. To confirm that there were no group differences in the ability of perceptual color discrimination during the study phase and to test for a potential increase in performance between pre- and post-training session, we conducted a 2 x 2 mixed measures ANOVA with the within subject factor *Session* (pre-training vs. post-training) and the between subject factor *Group* (training vs. control). The analysis revealed no significant effects or interactions, with the main effect Group, $F(1, 28) = 0.38, p = 0.544, \eta_p^2 = .01$, the main effect Session, $F(1, 28) = 0.46, p = 0.504, \eta_p^2 = .02$, and the interaction, $F(1, 28) = 0.08, p = 0.786, \eta_p^2 < .01$, indicating that the groups did not differ in their perceptual color discrimination ability and that performance in this task did not increase due to training.

To test for potential performance changes in perceptual color matching over the course of the training, we conducted a one-way analysis of variance (ANOVA) with the within subject factor *Run* (from pre-training session to the last training run 3b) for the training group. The ANOVA did not reach statistical significance, $F(7, 98) = 0.62, p = .574, \eta_p^2 = .04$, suggesting that the participants performed already at their best performance levels. This result highlights the suitability of perceptual color matching as study phase for the purpose of our experiment. Hence, no further analyses were conducted on the study phase of the VLTm task. Because we are mostly interested in the

recall of visual mental representations and not perceptual color matching, we will not further discuss these results.

Table 1

Average performance (deviation of the response color to the original color measured in degrees) in the VLTM study task, as a function of Group and Session. Values in parenthesis represent standard errors.

	day 1		day 2		day 3		day 4		day 5	
	pre-training		1a	1b	2a	2b	3a	3b	post-training	
training	3.42	(0.47)	3.13	(0.30)	3.38	(0.42)	3.70	(0.53)	3.45	(0.48)
control	3.21	(0.28)							3.33	(0.41)
									2.99	(0.20)

4.1.2 VLTM test. The test phase of the VLTM task was used to investigate the constitution of color representations retrieved from long-term memory. Baseline performance was assessed in the pre-training session. The task was further used as training task with identical object-color associations as during the pre-training session. A potential transfer of training benefits was assessed in the post-training session, where different objects and colors were used. Descriptive statistics for overall performance in the test phase of the VLTM task as a function of the different runs (pre-training to post-training) including the control group is depicted in Figure 2a. A power curve $y = a * x^b$, with y = overall performance in degrees, and x = session, was fit to performance of the training group across training runs (pre-training to run 3b). A non-linear least squares (NLS) model fit estimated an intercept, $a_{est} = 36.49$, $SD = 1.93$ and a slope, $b_{est} = -0.75$, $SD = 0.06$, both significantly different from zero with $t(103) = 18.96$, $p < 0.001$, and $t(103) = 11.84$, $p < 0.001$, respectively, indicating a good fit of observed performance to the power curve. The performance enhancement was also confirmed by a one-way

ANOVA with the within subject factor *Run* (pre-training to run 3b), which revealed a significant main effect, $F(7, 98) = 33.33, p < .001, \eta_p^2 = .70$. Subsequent *t*-tests for repeated measures showed a significant increase in performance from the pre-training session to the last training run 3b, $t(14) = 6.86, p < .001, d = 2.51$. Furthermore, an increase in performance was observed for the following comparisons: from the pre-training session to training run 1a, from run 1a to run 1b, and from run 1b to run 2a, all $ts(14) \geq 3.45$, all $ps \leq .004$, all $ds \geq 1.26$. There was also a trend for an increase in performance from run 2a to run 2b, $t(14) = 2.12, p = .053, d = 0.77$. Run to run improvements in overall performance after session 2b were not significant, all $ts(14) \leq 1.35$, all $ps \geq .199$, all $ds \leq 0.49$.¹

¹ Model-free analyses were repeated with means of absolute response errors for every participant (instead of medians). All statistical decisions were identical to those based on medians of absolute response errors, with the exception of an additional main effect Session, $F(1, 28) = 6.66, p = .015, \eta_p^2 = .19$, in the 2 x 2 mixed measures ANOVA for the VLTM data with the within-subject factor Session (pre-training vs. post-training) and the between-subject factor Group (training vs. control).

Figure 2. A) Average performance (deviation of the response color from the original color in degrees) of the VLTM test phase as a function of group and session. B) Average performance of the VSTM task as a function of group and session. Error bars represent standard errors.

To test for a potential transfer of benefits to different object-color associations, we computed a 2 x 2 mixed measures ANOVA with the within factor *Session* (pre-training vs. post-training) and the between subject factor *Group* (training vs. control). The analysis revealed a significant *Session* x *Group* interaction, $F(1, 28) = 6.63$, $p = .016$, $\eta_p^2 = .19$, due to an increase in performance from the pre-training to the post-training session in the training group, $t(14) = 3.38$, $p = .004$, $d = 1.24$, but not in the control group, $t(14) = 0.48$, $p = .637$, $d = 0.18$. The main effects in the ANOVA did not reach statistical significance, with *Session*, $F(1, 28) = 3.40$, $p = .076$, $\eta_p^2 = .11$, and *Group*, $F(1, 28) = 0.38$, $p = .540$, $\eta_p^2 = .01$.

4.1.3 VSTM. The VSTM task was conducted in the pre- and the post-training session to assess far transfer of the training effects to a different task, including different object-color associations. Descriptive statistics for the VSTM task are shown in Figure 2b. A two-factorial ANOVA for mixed measures with the within subject factor *Session* (pre-training vs. post-training) and the between subject factor *Group* (training vs. control) revealed a significant main effect *Session*, $F(1, 28) = 8.51, p = .007, \eta_p^2 = .23$, due to a general increase in performance from the pre-training to the post-training session. The interaction *Session* x *Group*, $F(1, 28) = 0.20, p = .662, \eta_p^2 = .01$, and the main effect *Group*, $F(1, 28) = 1.25, p = .273, \eta_p^2 = .04$, did not reach significance. Due to theoretical and practical reasons, we conducted paired sample *t*-tests to compare performance between sessions for each group separately. Interestingly, the training group showed a significant improvement in their overall performance from the pre-training to the post-training session, $t(14) = 3.10, p = .008, d = 1.13$. This was not the case for the control group, $t(14) = 1.47, p = .163, d = 0.54$. Hence, task repetition does not seem to be the only reason for the performance increase in the training group.

4.2 Estimated parameters

We aggregated the trials across participants for a given condition and fit the standard mixture model. Aggregated model fits per condition are depicted in Supplemental Figure 1.

4.2.1 Precision of VLTm. Aggregated MAPs and 95% Bayesian credible intervals for response precision (parameter *SD*) as a function of the different runs (pre-training to post-training) including the control group are shown in Figure 3a. The 95% credible intervals revealed a significant improvement in precision from the pre-training

session to the last training run 3b, $SD_{pre} = 29.87^\circ$, 95% CrI_{pre} : $[25.67^\circ, 35.66^\circ]$; $SD_{3b} = 15.93^\circ$, 95% CrI_{3b} : $[14.82^\circ, 17.12^\circ]$. Further inspection of the run to run increase in precision revealed significant increases from pre-training session to the first training run 1a, $SD_{pre} = 29.87^\circ$, 95% CrI_{pre} : $[25.67^\circ, 35.66^\circ]$; $SD_{1a} = 21.72^\circ$, 95% CrI_{1a} : $[19.86^\circ, 23.93^\circ]$, and from run 1b to run 2a, $SD_{1b} = 20.86^\circ$, 95% CrI_{1b} : $[19.24^\circ, 22.60^\circ]$; $SD_{2a} = 17.29^\circ$, 95% CrI_{2a} : $[16.06^\circ, 18.55^\circ]$. Other run to run comparisons were not significant. However, runs up to and with run 2a differed significantly from the last training run (3b), suggesting a slowing in the improvement in precision towards the last training run. Interestingly, run to run increases in precision were most pronounced between training runs which took place on different days. Thus, it seems possible to train fidelity of VLTm representations to a specific degree.

Figure 3. A) Aggregate parameter estimates of precision (standard deviation of the von Mises distribution) across trials of all participants for a given condition of the VLTm test phase. B) Aggregate parameter estimates of precision across trials of all participants for a given condition of the VSTM task. Error bars represent Bayesian 95% credible intervals.

To investigate the transfer of benefit in precision to new object-color associations, we compared the precision parameter as a function of *Session* (pre-training vs. post-training) and *Group* (training vs. control). This comparison revealed a significant improvement in the post-training session relative to the pre-training session for the training group, $SD_{\text{pre}} = 30.0^\circ$, 95% CrI_{pre}: [26.0°, 35.6°]; $SD_{\text{post}} = 23.6^\circ$, 95% CrI_{post}: [21.7°, 25.8°], but not for the control group, $SD_{\text{pre}} = 25.1^\circ$, 95% CrI_{pre}: [21.7°, 28.2°]; $SD_{\text{post}} = 22.2^\circ$, 95% CrI_{post}: [19.4°, 24.6°]. The result indicates that the effect of training on precision of VLTm representations can transfer to novel object-color associations, at least to a certain degree, and cannot solely be explained by means of task repetition.

Figure 4. Aggregate parameter estimates of the guess rate (probability of guessing) across trials of all participants for a given condition of the VLTM test phase. Error bars represent Bayesian 95% credible intervals.

4.2.2 Guess rate of VLTM. Aggregated MAPs and 95% Bayesian credible intervals for the proportion of guesses during the VLTM recall task for the different runs (pre-training to post-training) for the two groups (training, control) are depicted in Figure 4. Inspection of the 95% credible intervals of the training group revealed a significant decrease of guessing from the pre-training session to the last training run 3b, $g_{\text{pre}} = 0.43$, 95% CrI_{pre}: [0.36, 0.50]; $g_{3b} = 0.02$, 95% CrI_{3b}: [0.01, 0.04]. The decrease from training run to training run was significant until run 3b. Moreover, each run up to and with training run 2b differed significantly from the last training run 3b. The observed gradient suggests continuous improvements in the accessibility of the trained object-color associations over the course of the training.

We further compared the guess rate between pre-training and post-training session for the training group and for the control group. This comparison included the transfer to new object-color associations for both groups and revealed a significant improvement in the training group, $g_{\text{pre}} = 0.43$, 95% CrI_{pre}: [0.36, 0.50]; $g_{\text{post}} = 0.26$, 95% CrI_{post}: [0.22, 0.31], but not in the control group, $g_{\text{pre}} = 0.41$, 95% CrI_{pre}: [0.35, 0.47]; $g_{\text{post}} = 0.40$, 95% CrI_{post}: [0.36, 0.46]. Thus, training also leads to a transfer of benefits in the accessibility to untrained object-color associations.

4.2.3 Precision and guess rate of VSTM. As the training group enhanced their overall performance in the untrained VSTM task, we further estimated the parameters SD and g for this task. Due to low memory load, the guess rate in the VSTM task was close to zero in all conditions and thus, is not further analyzed or discussed. The aggregated MAPs and 95% Bayesian credible intervals of precision parameter SD as a function of session (pre-training vs. post-training) and group (training vs. control) are depicted in Figure 3b. The comparison of the 95% credible intervals revealed a significant increase in precision performance from pre- to post-session in the training group, $SD_{\text{pre}} = 16.7^\circ$, 95% CrI_{pre}: [15.7°, 17.7°]; $SD_{\text{post}} = 14.6^\circ$, 95% CrI_{post}: [13.7°, 15.5°], but not in the control group, $SD_{\text{pre}} = 14.6^\circ$, 95% CrI_{pre}: [13.8°, 15.6°]; $SD_{\text{post}} = 13.6^\circ$, 95% CrI_{post}: [12.8°, 14.4°]. These results indicate, that the effect of training in precision transferred to mental representations in an untrained task and cannot be explained by task repetition alone.

4.2.4 Precision of VLTm and VSTM representations. Due to the minimal memory load of one and the short maintenance interval of one second, the precision parameter in the VSTM (pre-training) task can be considered as representative baseline indicator for the maximum fidelity of mental representations, $SD_{\text{VSTM.Pre}} = 15.8^\circ$, 95%

$CrI_{VSTM.Pre}$: $[15.01^\circ, 16.8^\circ]$. The comparison of VLTm precision in the last training run 3b with VSTM precision in the pre-training session revealed no significant difference, $SD_{VLTm.3b} = 15.9^\circ$, 95% $CrI_{VLTm.3b}$: $[14.9^\circ, 17.2^\circ]$. In fact, the estimated precision parameters were virtually identical for VLTm representations and for VSTM representations. However, the comparison of the VLTm precision of the post-training session differed significantly from the precision of the VSTM task, $SD_{VLTm.Post} = 23.57^\circ$, 95% $CrI_{VLTm.Post}$: $[21.41^\circ, 26.04^\circ]$.

4.2.5 Reliability of parameter estimates. Averaged estimates of the parameters g and SD from the re-sampled data of each condition are listed in Table 2. Confirming the reliability of the parameter estimates from the original model fits across participants, all values were within the estimated Bayesian 95% credible intervals of the original model parameter estimates, with one exception (i.e., parameter g of the VSTM task in the pre-training session of the training group).

Table 2

Averaged parameter estimates for re-sampled data (i.e., 500 iterations). Values in parenthesis represent the lower and upper bounds of the Bayesian 95% credible intervals from the original parameter estimates of the aggregated trials across participants.

task	group	session	guess rate (g)		precision (SD)	
			M_{sampled}	95 % CrI	M_{sampled}	95% CrI
Test	training	1	0.430	[0.364; 0.497]	30.074	[26.001; 35.594]
		2	0.191	[0.152; 0.237]	21.805	[19.700; 23.917]
		3	0.105	[0.077; 0.135]	20.628	[19.231; 22.412]
		4	0.093	[0.067; 0.126]	17.343	[15.959; 18.802]
		5	0.058	[0.037; 0.082]	16.280	[15.316; 17.445]
		6	0.029	[0.014; 0.047]	16.628	[15.618; 17.762]
		7	0.023	[0.010; 0.043]	15.905	[14.924; 17.173]
		8	0.265	[0.217; 0.311]	23.616	[21.670; 23.754]
	control	1	0.407	[0.351; 0.471]	25.001	[21.679; 28.241]
		8	0.404	[0.358; 0.460]	22.180	[19.385; 24.644]
VSTM	training	1	0.005	[0.009; 0.038]	15.728	[15.703; 17.747]
		8	0.008	[0.002; 0.018]	14.536	[13.743; 15.487]
	control	1	0.008	[0.002; 0.022]	14.668	[13.784; 15.599]
		8	0.009	[0.004; 0.021]	13.605	[12.830; 14.368]

5. Discussion

Overall our data reveal that a relatively short training duration of less than an hour per day on three consecutive days enhances not only the accessibility of object-color associations stored in VLTm, but also the fidelity of their representations. Notably, at the end of the training fidelity of VTLM representations matched fidelity of a single object actively maintained in VSTM for a brief duration immediately after its presentation. Furthermore, training effects were not only observed for trained object-color associations but transferred to associations consisting of novel objects and colors and to a different task. Our findings suggest that training can affect the quality of visual mental representations.

At the end of our training, fidelity of mental representations retrieved from VLTM reached virtually the same level as the fidelity for one item maintained in VSTM over a short delay of one second. This result completes the previous observation, that fidelity of VLTM was similar to fidelity of VSTM, when the maximum capacity of VSTM was reached (Brady et al., 2013). Based on their results the authors suggested a common minimum on fidelity, which is needed that a mental representation is remembered. This minimal bound might be reached for example, when mental representations are stored and retrieved after delays longer than a few seconds, or when sustained maintenance over short delays is near the capacity limit of VSTM. Based on our observations, we suggest a common upper bound on fidelity, which stands for the highest possible fidelity a mental representation in visual memory can reach under optimal circumstances. Such circumstances are met, for instance, during sustained maintenance over short delays without interference (i.e., VSTM with a load of one) or, as we were able to demonstrate, with increasing expertise (i.e., after training) also for retrieval after longer delays. Thus, the bandwidth - from the minimum fidelity required for a mental representation to be remembered to the highest possible fidelity a mental representation can reach - seems to be identical for VSTM and VLTM.

The time course of the development of performance in the VLTM task across the training suggests an impact of consolidation processes from one day to the next day. The significant increases in performance overnight were especially pronounced for the precision parameter. By contrast, the guess rate improved mostly between the two runs within the first training session. Day-to-day consolidation on the guess rate was only observed after the first night. Particularly the observations for the precision parameter are

in line with research revealing consolidation during sleep in perceptual learning (e.g., Mednick, Nakayama, & Stickgold, 2003) or in episodic memory (e.g., Rasch & Born, 2013). Thus, our results suggest that not only accessibility but also fidelity of mental representations consolidate during sleep, supporting the notion that learning processes can affect the fidelity of visual mental representations in memory.

Two potential mechanisms need to be considered when explaining the observed training effect. The first is that training leads to more precise visual mental representations due to changes in neural areas shared with the visual system (i.e., perceptual learning). According to the assumption of a shared neural basis between mental representations and the visual system (e.g., Kosslyn et al., 1993; Pearson et al., 2015), this mechanism would involve neural adaptations in visual areas as in the associative cortex V4 which correlates with color perception (Zeki et al., 1991). The second is that training leads to learning on a semantic level. This mechanism would involve the development of semantic learning strategies, as for example applying more precise verbal labels to similar colors across the training (cf. Bae et al., 2015; Özgen & Davies, 2002; Souza & Skóra, 2017). It might be reasonable to assume that performance improvements with regards to accessibility was mainly driven by semantic learning strategies. By contrast, it seems less likely that strategies purely based on semantics led to the observed performance improvements in fidelity. This notion is supported by the fact that fidelity for mental representations of object-color associations stored in VLTM reached the same level of precision as fidelity for individual object-color associations in VSTM, which are unlikely to be actively maintained on an exclusive semantic basis.

Training effects transferred to novel object-color associations in the trained VLTM task and to different object-color associations in the untrained VSTM task. Although the transfer effect on fidelity was relatively small and hence, needs to be interpreted with caution, a comparison with the control group indicates that these benefits were not simply due to test repetition. At first glance, our findings might seem contradictory to the perceptual learning literature. In perceptual learning, training usually leads to a narrowing of the response patterns and effects of transfer are mostly non-existent or at best very restricted (cf. Goldstone, 1998; Karni & Bertini, 1997). On a neural level, perceptual learning leads to changes limited to brain areas associated with early visual processing, where cells become finer tuned and start to react more reliably to very specific stimulus characteristics, but less to similar characteristics (cf. Goldstone, 1998; Karni & Bertini, 1997). By contrast to stimuli of many perceptual learning paradigms, color perception is associated with processes in higher visual areas (V4; Zeki et al., 1991). Crucially, transfer can be observed under certain circumstances where perceptual learning is based on higher visual brain areas (Watanabe & Sasaki, 2015). Another potential explanation for the observed transfer of benefits is that, although our training was restricted to one specific perceptual feature (i.e., isoluminant colors), participants were trained on the whole spectrum of the available feature space. That is, on a neural level fine tuning occurred not only for a circumscribed part of the perceptual feature space, as is often the case in traditional perceptual learning paradigms, but in fact was applied to the entire space of the trained perceptual feature. Thus, it seems that transfer can occur when a trained feature space is paired with novel situations (e.g., as in our case objects and tasks).

A possible limitation of our research is the age difference between the experimental group and the control group. It is a well-documented fact that age negatively affects perception (e.g., visual acuity and color perception; cf. Knoblauch, Vital-Durand, & Barbur, 2001; Owsley, 2011, 2016; Paramei, 2012) and episodic memory (cf. Grady & Craik, 2000; Meier, Rey-Mermet, Rothen, & Graf, 2013). Furthermore, it is also well-documented that brain plasticity decreases with age (cf. Burke & Barnes, 2006; Park & Reuter-Lorenz, 2009). Although statistically significant, the age difference between the groups was not large enough to reveal a statistically significant impact on task performance in the pre-training session. Nevertheless, since the experimental group was older than the control group, the deck was stacked against our hypothesis that the fidelity of VLTm representations can be enhanced by means of training. That is, if anything, the age difference between the groups results in a conservative estimate of the training effects. Another limitation of our research might be the small number of trials per condition. Due to the small trial number, we fitted the standard mixture model of each condition across the pooled data of all participants. The cost of this approach is that variability between participants is not considered in the model estimates. However, the chosen approach does not challenge the reliability of our findings, as we demonstrated by means of a re-sampling approach. Furthermore, the main findings are supported by a model-free approach considering variability between participants.

To conclude, our results demonstrate that not only accessibility of mental representations can be enhanced by training but also their fidelity. At the end of the training, fidelity in VLTm was strikingly similar to fidelity in VSTM with a memory

load of one, suggesting common upper bounds (i.e., highest possible precision) on the fidelity of mental representations in the two memory systems. Thus, the observed pattern of results is unlikely to exclusively reflect semantic strategies but suggests that also perceptual learning processes are involved (i.e., tuning of cellular responses in visual brain areas). The observed benefit did not only occur for the trained object-color associations but transferred to novel object-color associations and to a different task. The results of a control group excluded the possibility that the observed changes in accessibility and fidelity could be attributed simply to repetition of the relevant tests. In summary, relatively short training on the entire space of a single perceptual feature can generate perceptual plasticity, resulting in enhanced fidelity of VLTm representations and a potential transfer of benefits to different contexts.

6. Acknowledgements

We thank Christoph Witzel for advice on color rendering. Further, we thank Geoffrey Ward, Jerry Fisher, and Christa von Dach for their helpful comments on a previous version of this article during a Summer School, and Esther Brill and Sophie Ankner for data acquisition.

7. Conflict of interest

On behalf of all authors, the corresponding author states that there is no conflict of interest.

References

- Allred, S. R., & Flombaum, J. I. (2014). Relating color working memory and color perception. *Trends in Cognitive Sciences*, 18(11), 562–565.
<http://doi.org/10.1016/j.tics.2014.06.002>
- Amar-Halpert, R., Laor-Maayany, R., Nemni, S., Rosenblatt, J. D., & Censor, N. (2017). Memory reactivation improves visual perception. *Nature Neuroscience*, 20(10), 1325–1328. <http://doi.org/10.1038/nn.4629>
- Baddeley, A. D., & Hitch, G. J. (2017). Is the Levels of Processing effect language-limited? *Journal of Memory and Language*, 92, 1–13.
<http://doi.org/10.1016/j.jml.2016.05.001>
- Bae, G.-Y., Olkkonen, M., Allred, S. R., & Flombaum, J. I. (2015). Why some colors appear more memorable than others: a model combining categories and particulars in color working memory. *Journal of Experimental Psychology: General*, 144(4), 744–763. <http://doi.org/10.1037/xge0000076>
- Bae, G.-Y., Olkkonen, M., Allred, S. R., Wilson, C., & Flombaum, J. I. (2014). Stimulus-specific variability in color working memory with delayed estimation. *Journal of Vision*, 14(4), 7–7. <http://doi.org/10.1167/14.4.7>
- Bennett, R. G., & Westheimer, G. (1991). The effect of training on visual alignment discrimination and grating resolution. *Perception & Psychophysics*, 49(6), 541–546.
<http://doi.org/10.3758/BF03212188>
- Brady, T. F., Konkle, T., Gill, J., Oliva, A., & Alvarez, G. A. (2013). Visual long-term memory has the same limit on fidelity as visual working memory. *Psychological Science*, 24(6), 981–990. <http://doi.org/10.1177/0956797612465439>

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, 10(4), 433–436.

<http://doi.org/10.1163/156856897X00357>

Brodeur, M. B., Dionne-Dostie, E., Montreuil, T., & Lepage, M. (2010). The bank of standardized stimuli (BOSS), a new set of 480 normative photos of objects to be used as visual stimuli in cognitive research. *PLoS ONE*, 5(5), e10773.

<http://doi.org/10.1371/journal.pone.0010773>

Burke, S. N., & Barnes, C. A. (2006). Neural plasticity in the ageing brain. *Nature Reviews Neuroscience*, 7(1), 30–40. <http://doi.org/10.1038/nrn1809>

Buschkuhl, M., Jaeggi, S. M., Mueller, S. T., Shah, P., & Jonides, J. (2017). Training change detection leads to substantial task-specific improvement. *Journal of Cognitive Enhancement*, 1, 419–433. <http://doi.org/10.1007/s41465-017-0055-y>

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*, 95(23), 13988–13993.

<http://doi.org/10.1073/pnas.95.23.13988>

Dosher, B. A., & Lu, Z.-L. (2017). Visual perceptual learning and models. *Annual Review of Vision Science*, 3, 343–363. <http://doi.org/10.1146/annurev-vision-102016-061249>

Fan, J. E., Hutchinson, J. B., & Turk-Browne, N. B. (2016). When past is present: Substitutions of long-term memory for sensory evidence in perceptual judgments. *Journal of Vision*, 16(8), 1. <http://doi.org/10.1167/16.8.1>

Fiorentini, A., & Berardi, N. (1980). Perceptual learning specific for orientation and spacial frequency. *Nature*, 287, 43–44.

- Fiorentini, A., & Berardi, N. (1981). Learning in grating waveform discrimination: Specificity for orientation and spatial frequency. *Vision Research*, 21(7), 1149–1158. [http://doi.org/10.1016/0042-6989\(81\)90017-1](http://doi.org/10.1016/0042-6989(81)90017-1)
- Fougnie, D., Suchow, J. W., & Alvarez, G. A. (2012). Variability in the quality of visual working memory. *Nature Communications*, 3, 1229. <http://doi.org/10.1038/ncomms2237>
- Goldstone, R. L. (1998). Perceptual learning. *Annual Review of Psychology*, 49, 585–612.
- Grady, C. L., & Craik, F. I. M. (2000). Changes in memory processing with age Cheryl L Grady* and Fergus IM Craik †. *Current Opinion in Neuro Biology*, 10, 224–231. <http://doi.org/10.1093/ejil/chq032>
- Karni, A., & Bertini, G. (1997). Learning plasticity. *Current Opinion in Neuro Biology*, 7, 530–535.
- Knoblauch, K., Vital-Durand, F., & Barbur, J. L. (2001). Variation of chromatic sensitivity across the life span. *Vision Research*, 41(1), 23–36. [http://doi.org/10.1016/S0042-6989\(00\)00205-4](http://doi.org/10.1016/S0042-6989(00)00205-4)
- Konkle, T., Brady, T. F., Alvarez, G. A., & Oliva, A. (2010). Conceptual Distinctiveness Supports Detailed Visual Long-Term Memory for Real-World Objects. *Journal of Experimental Psychology: General*, 139(3), 558–578. <http://doi.org/10.1037/a0019165>
- Kosslyn, S. M., Alpert, N. M., Thompson, W. L., Maljkovic, V., Weise, S. B., Chabris, C. F., ... Buonanno, F. S. (1993). Visual mental imagery activates topographically organized visual cortex: PET investigations. *Journal of Cognitive Neuroscience*, 5(3), 263–287. <http://doi.org/10.1162/jocn.1993.5.3.263>

- Leys, C., Ley, C., Klein, O., Bernard, P., & Licata, L. (2013). Detecting outliers: do not use standard deviation around the mean, use absolute deviation around the median. *Journal of Experimental Social Psychology*, 49(4), 764–766.
<http://doi.org/10.1016/j.jesp.2013.03.013>
- Mast, F. W., Tartaglia, E. M., & Herzog, M. H. (2012). New percepts via mental imagery? *Frontiers in Psychology*, 3, 360. <http://doi.org/10.3389/fpsyg.2012.00360>
- Mednick, S., Nakayama, K., & Stickgold, R. (2003). Sleep-dependent learning: a nap is as good as a night. *Nature Neuroscience*, 6(7), 697–698.
<http://doi.org/10.1038/nn1078>
- Meier, B., Rey-Mermet, A., Rothen, N., & Graf, P. (2013). Recognition memory across the lifespan: the impact of word frequency and study-test interval on estimates of familiarity and recollection. *Frontiers in Psychology*, 4, 1–15.
<http://doi.org/10.3389/fpsyg.2013.00787>
- Owsley, C. (2011). Aging and vision. *Vision Research*, 51(13), 1610–1622.
<http://doi.org/10.1016/j.visres.2010.10.020>
- Owsley, C. (2016). Vision and aging. *Annual Review of Vision Science*, 2, 255–271.
<http://doi.org/10.1146/annurev-vision-111815-114550>
- Özgen, E., & Davies, I. R. L. (2002). Acquisition of categorical color perception: a perceptual learning approach to the linguistic relativity hypothesis. *Journal of Experimental Psychology: General*, 131(4), 477–493. <http://doi.org/10.1037//0096-3445.131.4.477>
- Paramei, G. V. (2012). Color discrimination across four life decades assessed by the Cambridge Colour Test. *Journal of the Optical Society of America A*, 29(2), A290–

A297. <http://doi.org/10.1364/JOSAA.29.00A290>

Park, D. C., & Reuter-Lorenz, P. (2009). The adaptive brain: aging and neurocognitive scaffolding. *Annual Review of Psychology*, 60(1), 173–196.

<http://doi.org/10.1146/annurev.psych.59.103006.093656>

Pearson, J., Clifford, C. W. G., & Tong, F. (2008). The functional impact of mental imagery on conscious perception. *Current Biology*, 18(13), 982–986.

<http://doi.org/10.1016/j.cub.2008.05.048>

Pearson, J., Naselaris, T., Holmes, E. A., & Kosslyn, S. M. (2015). Mental imagery: functional mechanisms and clinical applications. *Trends in Cognitive Sciences*,

19(10), 590–602. <http://doi.org/10.1016/j.tics.2015.08.003>

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: transforming numbers into movies. *Spatial Vision*, 10(4), 437–442.

<http://doi.org/10.1163/156856897X00366>

Prinzmetal, W., Amiri, H., Allen, K., & Edwards, T. (1998). Phenomenology of attention:

I. Color, location, orientation, and spatial frequency. *Journal of Experimental Psychology: Human Perception and Performance*, 24(1), 261–282.

<http://doi.org/10.1037/0096-1523.24.1.261>

Rademaker, R. L., & Pearson, J. (2012). Training visual imagery: improvements of metacognition, but not imagery strength. *Frontiers in Psychology*, 3, 224.

<http://doi.org/10.3389/fpsyg.2012.00224>

Rajaram, S. (1996). Perceptual effects on remembering: recollective processes in picture recognition memory. *Journal of Experimental Psychology. Learning, Memory, and Cognition*, 22(2), 365–377.

- Rasch, B., & Born, J. (2013). About sleep's role in memory. *Physiological Reviews*, 93, 681–766. <http://doi.org/10.1152/Physrev.00032.2012>
- Schoups, A. A., Vogels, R., & Orban, G. A. (1995). Human perceptual learning in identifying the oblique orientation: retinotopy, orientation specificity and monocularity. *The Journal of Physiology*, 483(3), 797–810. <http://doi.org/10.1113/jphysiol.1995.sp020623>
- Schoups, A. A., Vogels, R., Qian, N., & Orban, G. (2001). Practising orientation identification improves orientation coding in V1 neurons. *Nature*, 412(6846), 549–553. <http://doi.org/10.1038/35087601>
- Souza, A. S., & Skóra, Z. (2017). The interplay of language and visual perception in working memory. *Cognition*, 166, 277–297. <http://doi.org/10.1016/j.cognition.2017.05.038>
- Suchow, J. W., Brady, T. F., Fougner, D., & Alvarez, G. A. (2013). Modeling visual working memory with the MemToolbox. *Journal of Vision*, 13(10), 9. <http://doi.org/10.1167/13.10.9.doi>
- Sutterer, D. W., & Awh, E. (2016). Retrieval practice enhances the accessibility but not the quality of memory. *Psychonomic Bulletin and Review*, 23(3), 831–841. <http://doi.org/10.3758/s13423-015-0937-x>
- Tartaglia, E. M., Bamert, L., Mast, F. W., & Herzog, M. H. (2009). Human perceptual learning by mental imagery. *Current Biology*, 19(24), 2081–2085. <http://doi.org/10.1016/j.cub.2009.10.060>
- Thurston, C., & Dobkins, K. (2007). Stimulus-specific perceptual learning for chromatic, but not luminance, contrast detection. *Journal of Vision*, 7(9), 469–469.

- van den Berg, R., Shin, H., Chou, W.-C., George, R., & Ma, W. J. (2012). Variability in encoding precision accounts for visual short-term memory limitations. *Proceedings of the National Academy of Sciences*, 109(22), 8780–8785.
<http://doi.org/10.1073/pnas.1117465109>
- Vingrys, A. J., & King-Smith, P. E. (1988). A quantitative scoring technique for panel tests of color vision. *Investigative Ophthalmology and Visual Science*, 29(1), 50–63.
- Wang, F., Zhong, X., Huang, J., Ding, Y., & Song, Y. (2013). Comparison of perceptual learning of real and virtual line orientations: an event-related potential study. *Vision Research*, 93, 1–9. <http://doi.org/10.1016/j.visres.2013.10.004>
- Watanabe, T., & Sasaki, Y. (2015). Perceptual learning: toward a comprehensive theory. *Annual Review of Psychology*, 66(1), 197–221. <http://doi.org/10.1146/annurev-psych-010814-015214>
- Wesemann, W., Schiefer, U., & Bach, M. (2010). Neue DIN-Normen zur Sehschärfebestimmung. *Ophthalmologe*, 107(9), 821–826.
<http://doi.org/10.1007/s00347-010-2228-2>
- Wilken, P., & Ma, W. J. (2004). A detection theory account of change detection. *Journal of Vision*, 4(12), 11. <http://doi.org/10.1167/4.12.11>
- Witzel, C., & Franklin, A. (2014). Do focal colors look particularly “colorful”? *Journal of the Optical Society of America A*, 31(4), A365–A374.
<http://doi.org/10.1364/JOSAA.31.00A365>
- Xie, W., & Zhang, W. (2017). Negative emotion enhances mnemonic precision and subjective feelings of remembering in visual long-term memory. *Cognition*, 166, 73–83. <http://doi.org/10.1016/j.cognition.2017.05.025>

- Xie, W., & Zhang, W. (2018). Mood-dependent retrieval in visual long-term memory: dissociable effects on retrieval probability and mnemonic precision. *Cognition and Emotion*, 32(4), 674–690. <http://doi.org/10.1080/02699931.2017.1340261>
- Zeki, S., Watson, J. D. G., Lueck, C. J., Friston, K. J., Kennard, C., & Frackowiak, R. S. J. (1991). A direct demonstration of functional specialization in human visual cortex. *The Journal of Neuroscience*, 11(3), 641–649.
- Zhang, W., & Luck, S. J. (2008). Discrete fixed-resolution representations in visual working memory. *Nature*, 453, 233–235. <http://doi.org/Doi 10.1038/Nature06860>