**Practice Makes It Better:**

A Psychophysical Study of Visual Perceptual Learning and Its Transfer Effects on Aging

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Abstract

Previous studies on perceptual learning, acquiring a new skill through practice, appear to stimulate brain plasticity and enhance performance (Fiorentini & Berardi, 1981). The present study aimed to determine (1) whether perceptual learning can be used to compensate for age-related declines in perceptual abilities, and (2) whether the effect of perceptual learning can be transferred to untrained stimuli and subsequently improve capacity of visual working memory (VWM). We tested both healthy younger and older adults in a three-day training session using an orientation discrimination task. A matching-to-sample psychophysical method was used to measure improvements in orientation discrimination thresholds and reaction times (RTs). Results showed that both younger and older adults improved discrimination thresholds and RTs with similar learning rates and magnitudes. Furthermore, older adults exhibited a generalization of improvements to three untrained orientations that were close to the training orientation and benefited more comparing to younger adults from the perceptual learning as they transferred learning effects to the VWM performance. We conclude that through perceptual learning, older adults can partially counteract age-related perceptual declines, generalize the learning effect to other stimulus conditions, and further overcome the limitation of using VWM capacity to perform a perceptual task.

Key words: perceptual learning, aging, visual perception, generalization, visual working memory

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A number of perceptual abilities are diminished with increasing adult age, which has the potential to place the elderly at risk for personal injury (for reviews, see Andersen, 2012; Owsley, 2011; Werner, Schefrin, & Bradley, 2010). Neurophysiological research has shown that age-related declines in visual perception are associated with weaker orientation selectivity in the primary visual cortical cells in older cats and rhesus monkeys (Hua et al., 2006; Yu, Wang, Li, Zhou, & Leventhal, 2006), suggesting that age-related changes in cortical processing are the underlying mechanism that contributes to age-related declines in visual perception (Andersen, 2012).

One promising approach to improving vision in healthy adults is perceptual learning, in which observers are repeatedly exposed to a specific stimulus or task through training. Recent studies found that perceptual learning improved older adults’ performance on an orientation discrimination task (e.g., Betts, Sekuler, & Bennett, 2007; Deloss, Watanabe, & Andersen, 2014, 2015), suggesting perceptual learning might stimulate neural plasticity (Boyke, Driemeyer, Gaser, Büchel, & May, 2008). However, these studies used relatively simple orientation discrimination tasks (e.g., determining whether a stimulus rotated clockwise or counterclockwise from the horizontal orientation). It is possible that the improvement might be limited to simple tasks.

The present study therefore examined whether the benefit of perceptual learning for older adults persists with a high working-memory-load task. We adopted a matching-to-sample task, in which two high-contrast stimuli were simultaneously presented as the target set, followed by a subsequent probe. Participants decided which of the two target orientations matched the probe
(Macmillan & Creelman, 2005). This task required both encoding and storing the identity and position of two targets in the first interval, and matching the stored target orientations to that of the subsequently presented probe. Thus, the baseline performance prior to perceptual learning was likely to be lower than that observed in previous studies (e.g., Deloss et al., 2014, 2015), resulting in more room for training-based improvement for older adults. We further examined whether perceptual learning enabled transfer to higher-level cognitive functions using a three-day training program. This design allowed us to assess whether perceptual learning in older adults originates from changes in either early or midlevel representations of visual processing.

Perceptual Learning and Aging

Given the broad declines in visual functions with age, several recent studies have applied perceptual learning to older adults. For instance, Polat et al. (2012) had older adults with presbyopia perform a contrast detection task and found that the training substantially attenuated age-related declines in visual acuity, spatial and temporal contrast sensitivity, contrast discrimination abilities, and reading speed for small letters. Similar learning-based improvements were found in other object discrimination and detection tasks for healthy older adults (Andersen, Ni, Bower, & Watanabe, 2010; Ball & Sekuler, 1986; McKendrick & Battista, 2013). Furthermore, these studies have found that perceptual learning in older adults was similar to that in younger adults in learning rates, magnitudes, and retention. Therefore, these studies provide evidence that perceptual learning improves visual functions in healthy older adults.

Early studies have shown that effects of perceptual learning are restricted to a specific orientation, retinotopic location, spatial frequency, and eye of origin (for reviews, see Lu, Hua, Huang, Zhou, & Dosher, 2011; Sagi, 2011). This specificity of perceptual learning suggests that it affects neural processing at an early stage of visual processing, such as V1 (Sagi, 2011).
However, other studies have shown that learning can be transferred to a new retinotopic location that was primed prior training, suggesting that perceptual learning might alter an intermediate-level coding (e.g., location-independent representations; see e.g., Xiao et al., 2008; Zhang, Xiao, Klein, Levi, & Yu, 2010; Zhang et al., 2010). One question remained to be answered is whether perceptual learning for older adults occurs in either early or midlevel representations of visual processing.

**Orientation Discrimination and Training**

Orientation discrimination ability, commonly studied in perceptual learning is assessed using a forced-choice, psychophysical method. For instance, Betts et al. (2007, Experiment 2) used an one-alternative forced choice (1AFC) task, in which observers reported whether a stimulus was rotated clockwise or counter-clockwise from the horizontal orientation. Results showed that older adults compared to younger adults had higher orientation discrimination thresholds (as an index of individual’s just-noticeable difference between these two stimulus orientations) when stimulus contrast was low, but equivalent thresholds when stimulus contrast was high. These findings suggest that internal noise increased with age. Early studies have demonstrated that orientation discrimination ability in younger adults improves with one day of practice (Vogels & Orban, 1985), or five or more days of perceptual training (Dosher & Lu, 1998; Matthews, Liu, Geesaman, & Qian, 1999; Matthews, Liu, & Qian, 2001; Schoups, Vogels, & Orban, 1995). Deloss et al. (2015; see also 2014) further found that perceptual learning facilitated orientation discrimination in older adults. In their study, both younger and older adults received 7 days of training on a 2AFC orientation discrimination task, in which they determined whether a target stimulus was rotated clockwise or counter-clockwise from a probe stimulus with a chosen training orientation. To examine the effect of stimulus noise on perceptual learning,
Deloss et al. manipulated the Gaussian noise in stimuli. They found that older adults achieved a level of orientation discrimination thresholds after training similar to younger adults prior to training. Also, they proposed that training enabled a transfer of the improvement of orientation discrimination thresholds to an untrained orientation that was 50° off the training orientation. Older adults also showed greater improvements in thresholds in the high-stimulus-noise conditions as compared to younger adults, but there were no age differences in improvement for the low-noise condition.

Although Deloss et al. (2015) reported transfer effects from perceptual learning of orientation discrimination, it is difficult to determine what actually caused their transfer effects. First, there was no control group to assess the absence of training on perceptual learning. It is possible that their transfer effect was due to task practice before the training (i.e., Day 1—when both trained and untrained orientations were included). Because changes of orientation discrimination thresholds on the untrained orientation condition were measured with the same orientation discrimination task used for the trained orientation condition, the transfer effect could be due to familiarity of the task with practice. Other studies examining aging and perceptual learning (Andersen et al., 2010; Deloss et al., 2014) have used training with suprathreshold stimuli to equate task practice across training and control groups so that the observed training effect in the training group could not be explained by task practice. However, this approach cannot rule out the possibility that the transfer effect was caused by task practice on Day 1. Finally, no Age × Testing Day × Orientation (trained, untrained) interaction was reported. Thus, an inclusion of a control group is necessary for examining whether transfer effects on the untrained orientation are due to the training itself, as claimed by Deloss et al. (2015) or the task practice on Day 1.
Transfer Effects

The perceptual learning of orientation discrimination has been found to increase the slopes of orientation tuning functions of neurons whose preferred orientations are 12°–20° away from a training orientation (Schoups, Vogels, Qian, & Orban, 2001). Meanwhile, the estimated bandwidth of orientation tuning functions in early cortical areas is approximately 30°–40° (Campbell & Kulikowski, 1966; McAdams & Maunsell, 1999). Thus, untrained orientations that are close enough to fall in the orientation tuning functions of training-target neurons (e.g., neurons that are tuned to orientations 12°–20° away from the training orientation) should also be affected by the same perceptual-learning-triggered changes in the slopes of the orientation tuning functions. In other words, the learning effect should transfer to these untrained orientations because neural representations of new orientations are similar as those of the training orientation. This notion of transfer of learning within the same feature channel (e.g., orientation tuning function) has been demonstrated in a push-pull perceptual learning task. For example, significant learning effects (i.e., reduction in sensory eye dominance) were found on four training orientations (e.g., 0°, 45°, 90°, and 135°) as well as on two untrained orientations (e.g., 22.5° and 67.5°; Xu, He, & Ooi, 2012). But this notion has not been tested with older adults, except that older adults in Deloss et al. (2015) showed a transfer effect to an orientation that was 50° off the training orientation. However, as discussed above, their finding was susceptible to an alternative explanation (i.e., Day-1 practice) due to the lack of control groups. Also, this transfer effect was tested only on one untrained orientation. It is unknown whether the effect can be consistently observed with different untrained orientations.

Age-Related Differences in Visual Working Memory
Converging behavioral evidence suggests that normal aging is associated with considerable declines in visual working memory (VWM; Park & Gutchess, 2003; Reuter-Lorenz & Sylvester, 2005; West, 2004). Although working memory training in older adults is effective (Karbach & Verhaeghen, 2014), older adults tend to exhibit limited transfer of improvements in dual-task performance through single-task practice (Maquestiaux, Laguë-Beauvais, Ruthruff, Hartley, & Bherer, 2010).

Recent studies, however, have found that perceptual learning of a motion discrimination task could eliminate age differences in VWM (Berry et al., 2010; Mishra, Rolle, & Gazzaley, 2015). In Berry et al., participants performed a contracted/expanded discrimination task on Gabor-pattern stimuli for three to five weeks. They found that trained participants showed significant improvement after training in both speed and detection accuracy relative to no-training participants. Also, participants’ performance (accuracy) on an untrained delayed-motion discrimination task with random-dot-pattern stimuli significantly improved after training. Furthermore, this training effect was eliminated when tested at a new perceptual threshold. These findings suggest that improvements in VWM performance could be partially induced by training-induced perceptual enhancement. An event-related potential (ERP) study by Mishra et al. (2015) revealed that early visual ERP components (N1 and N2), an index of attention allocation, were enhanced after the training for older adults. They suggested that training primarily enhances older adults’ ability in attention allocation. However, the VWM task used in both studies involved processing a single feature (i.e., the direction of moving Gabor or random-dot patterns). It is possible that improvement in VWM performance for older adults is limited to easy VWM tasks.

**The Present Study**
There are several issues of interest in the present study. First, we chose to measure orientation discrimination thresholds on high-contrast stimuli with a matching-to-sample task. In each trial, two high-contrast stimuli were presented simultaneously as the target set, followed by a subsequent probe. Participants decided which of the two target orientations matched the probe. To perform this task, one could attempt to encode both stimuli in the first interval and select the subsequent stimulus that matched the probe stimulus. This task demands cognitive resources not only for encoding the identity and position of two targets in the first interval but also for matching target orientations to that of the probe. With time constraints, the task is thought to be more difficult than the 1AFC/2AFC task used in the previous studies. Thus, we expect the baseline performance prior to perceptual training (Day 1) to be lower in the present study than that observed in previous studies (Betts et al., 2007; Deloss et al., 2014, 2015). This lower baseline would create more room for improvement through the training, making our study more sensitive to the effect of perceptual learning in older adults.

Second, while Deloss et al. (2015) claimed to successfully apply perceptual learning to improve orientation discrimination in older adults with a 2AFC task (Deloss et al., 2015), they did not include a control group nor did they report the results across their training sessions. Thus, we aimed to replicate Deloss et al. using a similar task but included control groups and examined performance across training days. Both younger and older adults received a three-day training program. Control groups received baseline (Day 1) and Time 2 (Day 5) assessments, but not the three-day training. We predicted that perceptual learning would significantly improve the orientation discrimination ability for both age groups (as measured by comparing performances from Day 1 and Day 5). As a result of perceptual learning, age differences in orientation discrimination performance should decline. Furthermore, we predicted that older adults exhibited
similar magnitudes and rates of perceptual learning compared to younger adults due to the low-noise stimulus condition.

Third, the present study assessed the transfer effect to four untrained orientations that were close to the training orientation for younger and older adults. Two of these four untrained orientations were 22.5° and 67.5° that were 22.5° rotated away from the 45° training orientation, and the other two were 0° and 90° that were 45° rotated away from the 45° training orientation. We predicted a transfer effect at orientations that were 22.5° tilted from the training orientation and a relatively small or no transfer at orientations that were 45° tilted from the training orientation. It is hypothesized that if we trained with a 45° grating stimuli, it would be more likely to induce a substantial learning effect in neurons optimally tuned to 22.5° and 67.5°. Although both 0° and 90° cardinal orientations may have different baseline thresholds than other non-cardinal orientations (e.g., 22.5°, 67.5°, and 45°), this does not preclude a possibility that training with 45° grating stimuli might also induce a learning effect on neurons with their orientation tuning functions with most spike activities at 0° and 90°. It is possible that these neurons can still be activated by the 45° grating stimuli, though with reduced activity rates, due to an increase in the intensity of the training (e.g., increased attention effort; Xu et al., 2012).

Fourth, we investigated whether perceptual enhancement induced by perceptual learning would transfer to the higher-VWM-demand task for younger and older adults. We changed the inter-stimulus interval (ISI) from 400 ms in the original orientation discrimination task to 1,500 ms. With this longer ISI, participants might require more VWM demands for maintaining visual information obtained from the first interval. The VWM demand is important for determining if a perceptual training program has an impact on higher cognitive functions.

**Method**
Participants

We recruited 20 younger and 20 older adults for the training condition who received three consecutive days of training, as well as pre-training and post-training assessments. Another 12 younger and 12 older adults served as controls who received pre-training and post-training assessments but not the training. Older participants (60–86 years old) were recruited from the Akron-area community and were paid up to $100. Younger adults (18–35 years old) were University of Akron undergraduates who were given course credit for participation. All the participants had no history of psychiatric or neurological disorders. Table 1 shows participants’ demographic information as well as perceptual and cognitive test results. As expected, older adults were slower in processing speed but showed higher vocabulary scores compared to younger adults for both tests ($p$s < .05). Years of education were matched between younger and older participants for both training and control conditions ($p$s > .05).

Apparatus and Stimuli

Visual stimuli were sine-wave grating disks, generated by the PsychToolbox-3 (Brainard, 1997; Pelli, 1997) in Matlab (R2012b version) for Mac OS X (version 10.8). The visual stimuli were displayed on a CRT monitor (DELL M991, resolution: 1280 × 1024 pixels, refresh rate: 85 Hz) at an 85-cm viewing distance. Participants were given a chin rest for stabilizing head positions and requested to binocularly observe visual stimuli. All the tests were run in a darkened room. The grating stimuli (GSs) ($3^\circ$ of visual angle, spatial frequency = 3 cpd, mean luminance = 50 cd/m$^2$, 1.5 log unit for contrast, the phase relative to the center of the stimulus was fixed at $0^\circ$) were displayed against a gray homogeneous background (luminance = 50 cd/m$^2$). The fixation cross (image size = $0.45^\circ \times 0.45^\circ$, line width = $0.1^\circ$, luminance = 70 cd/m$^2$) was used for
participants’ fixation at the center of the screen. A checkerboard sinusoidal grating was displayed as a mask at the end of each trial (7.5° × 7.5°, 3 cpd, 50 cd/m², 1.5 log unit).

Procedure

**Orientation discrimination task.** Orientation discrimination thresholds were measured with the matching-to-sample task (Macmillan & Creelman, 2005). Figure 1a shows an event sequence. In the first interval, a GS with a reference orientation (RO) and another GS with an orientation that was tilted counter-clockwise from the RO with an orientation increment (RO + ΔO) were displayed at 2° (visual angle) above and below the fixation cross (see Figure 1b). The order of locations of two GSs was randomized within a block. In the second interval, the probe GS, either the reference GS or the tilted one, was presented in the center of the screen. Participants were to quickly and accurately press the “1” or “2” key for the top or bottom GS, respectively, in the first interval that had the same orientation as the probe GS. An auditory feedback with a high or low pitch was provided to inform whether the response was correct or wrong. The QUEST method (Watson & Pelli, 1983, see Supplemental Materials for details) was used to adjust the orientation increment for each trial and to estimate the orientation discrimination threshold for each block (50 trials/block).

**Visual working memory (VWM) task.** To examine whether the perceptual learning improves the VWM capacity in general, the same orientation discrimination task was administered before and after the training phase except that the ISI between the two GSs and the probe GS was extended from 400 ms to 1,500 ms.

**General test procedure.** The five-day experiment consisted of one day of testing for before-training assessment, three training sessions (one session/day), and one day of testing for after-training assessment. The before- and after-training assessments included: (a) the orientation
discrimination task in which RO was set at the training orientation (= 45°); (b) the same orientation discrimination tasks in which a pair of two untrained orientations was used as ROs; and (c) the VWM task (in which RO = 45°). The untrained orientations were 90° and 0° (training orientation ± 45°) and 22.5° and 67.5° (training orientation ± 22.5°) (Figure 1c). We randomly selected 10 participants from each age group in the training condition to measure changes in orientation discrimination thresholds on a pair of untrained orientations (90° and 22.5°), while the other 10 participants were tested on the other pair (0° and 67.5°). Likewise, 6 participants randomly selected from each age group in the control condition were tested on the 90°-22.5° pair while the other 6 participants were tested on the 0°-67.5° pair. Two blocks (50 trials/block) were repeated with each RO in the orientation discrimination tasks and the VWM task. The order of these tasks was randomized determined for each participant. The three-day training sessions contained 2,400 trials of the orientation discrimination task (with RO = 45°), in which each session contained 16 blocks (50 trials/block). Each session lasted for approximately 1.5 hours. Participants were provided with a one-minute break between each block and a five-minute break every eight blocks to prevent fatigue.

**Data screening.** Participants’ reaction times (RTs) were recorded from the onset of the probe until the time when a participant pressed a response key. Data were filtered by removing incorrect trials as well as trials in which RTs were less than 10 ms or greater than 2,000 ms and more than 3-SDs above or below the participant’s mean RT within each block (see details in Supplemental Materials). The remaining trials were used for final analyses reported below.

**Results**

Within each age group, it was confirmed that training and control participants were equivalent in their orientation discrimination thresholds and RTs at the training orientation prior
to the training (see details in Table S1 in Supplemental Materials). Prior to the training, older adults had higher mean orientation discrimination thresholds and longer RTs than younger adults in the original orientation discrimination task at the training orientation and also in the VWM task (see details in Table S1).

**Improvements on the training orientation as a result of perceptual learning.** To examine the effect of perceptual learning, mean orientation discrimination thresholds for the RO of 45° from before- and after-training assessments were subjected to an Age (younger and older) × Group (training and control) × Time (before-training and after-training) ANOVA. This ANOVA showed a non-significant Age × Group × Time interaction but a significant Group × Time interaction (Table 2). After splitting the data by age, and two-way, simple-effect ANOVAs were run on each of age groups separately. These ANOVAs showed a significant Group × Time interaction for both younger and older adults. As shown in Figure 2a, the older training group showed a significant improvement on the orientation discrimination thresholds ($F(1, 19) = 75.43, p < .001, \eta^2_p = .80$), whereas the older control group did not ($F(1, 11) = 3.43, p = .09, \eta^2_p = .24$). Likewise, the younger training group showed a significant improvement in the orientation discrimination threshold ($F(1, 19) = 47.05, p < .001, \eta^2_p = .71$). Different from the older control group, the younger control group also significantly improved the thresholds over the time ($F(1, 11) = 6.05, p = .032, \eta^2_p = .36$). However, as indicated by the significant Group × Time interaction for younger adults ($F(1, 30) = 12.20, p = .002, \eta^2_p = .29$), threshold improvements in the younger control group, if any, were not as strong as those in the younger training group.

The mean reductions in orientation discrimination thresholds showed no significant age difference between younger and older training groups, $t(38) = -1.139, p = .26, d = .36$. Furthermore, after the training, older participants achieved the same level of orientation
discrimination performance as pre-training younger adults, \( t(38) = .410, p = .68, d = .13 \). These results indicate that through the three-training-session perceptual learning, older participants improved their orientation discrimination thresholds in the same magnitude as younger training participants, and then reached a comparable discrimination threshold relative to younger adults before training.

Changes in mean thresholds were also analyzed for training groups over the course of the entire five-day experiment. The mean thresholds reduced gradually as the training progressed across the five days for both younger training group (slope = -1.40, \( R^2 = .87, F(1, 4) = 20.18, p = .021 \)) and older training group (slope = -1.81, \( R^2 = .94, F(1, 4) = 44.34, p = .007 \)) (Figure 2b). The mean slopes between the younger and older training groups showed no significant age difference, \( t(38) = 1.42, p = .16, d = .45 \), suggesting that both age groups showed similar rates of training-based improvements in the orientation discrimination thresholds.

To assess the training effect on the response speed, RTs were analyzed in the same manner as orientation discrimination thresholds (see Table 2 for a summary of the ANOVA) The Group × Time interaction was significant for both younger and older adults. As shown in Figure 2c, the younger training group showed a significant decrease in RTs, \( F(1, 19) = 11.28, p = .003, \eta_p^2 = .37 \), whereas the younger control group did not, \( F < 1 \). Likewise, the older training group showed a significant decrease in RTs, \( F(1, 19) = 35.40, p < .001, \eta_p^2 = .65 \), whereas the older control group did not, \( F < 1 \). Reductions in mean RTs did not show a significant age difference between the older and younger training groups, \( t(18) = -.89, p = .41, d = .26 \). Furthermore, after the training, older participants achieved the same level of RTs as pre-training younger adults, \( t(38) = .42, p = .68, d = .13 \). As plotted in Figure 2d, changes of mean RTs across five days of sessions showed a linear reduction for both the older training group (slope = -50.31, \( R^2 = .94 \),
F(1, 4) = 48.72, p = .006) and the younger training group (slope = -39.49, R^2 = .79, F(1, 4) = 11.41, p = .043). The mean slopes between the younger and older training groups showed no significant age difference, t(18) = .78, p = .44, d = .25. Overall, both younger and older adults who underwent the training improved their perceptual discriminability and processing speed in the same magnitude and learning rate. Most importantly, after the training, older participants achieved the same level of RTs as pre-training younger adults, t(38) = .42, p = .68, d = .13, suggesting that training could assist older adults to reach comparable discrimination thresholds and RTs as younger adults who did not receive the training.

**Effects of perceptual learning on untrained orientations.** The effect of transferring perceptual learning effects on untrained orientations was measured when ROs were 90° and 0°, which were 45° rotated from the training orientation, as well as when ROs were 22.5° and 67.5°, which were 22.5° rotated from the training orientation. For orientation discrimination thresholds, there were no training-based improvements on the untrained orientation (RO = 90°) (Fs < 1.21, ps > .28, ηp^2s < .04, Figure 3d). Table 3 shows results for other untrained orientations. When RO was 22.5°, the Group × Time interaction was significant for older adults but not for younger adults. The older training group significantly improved thresholds on the untrained orientation of 22.5°, F(1, 9) = 14.99, p = .004, ηp^2 = .63, whereas the older control did not, F < 1 (Figure 3a).

When RO was 67.5°, both younger and older adults showed a significant Group × Time interaction. The older training group significantly improved thresholds (F(1, 9) = 17.35, p = .002, ηp^2 = .66) relative to the control group (F < 1) (Figure 3b). Also, the younger training group significantly improved thresholds (F(1, 9) = 10.08, p = .011, ηp^2 = .53), but the younger control group did not (F < 1). However, reductions in mean thresholds when RO was 67.5° in the older
training group were significantly greater than those in the younger training group, $t(18) = -2.25$, $p = .037$, $d = 1.01$.

When RO was $0^\circ$, the Age × Group × Time interaction was significant. This result occurred because older adults showed a significant Group × Time interaction ($F(1, 14) = 6.93$, $p = .020$, $\eta_p^2 = .33$) whereas younger adults did not ($F(1, 14) = .10$, $p = .76$, $\eta_p^2 = .007$). The older training group significantly improved thresholds on the untrained orientation of $0^\circ$, $F(1, 9) = 6.29$, $p = .033$, $\eta_p^2 = .41$, whereas the older control did not, $F(1, 5) = 2.39$, $p = .18$, $\eta_p^2 = .32$ (Figure 3c). These results suggest that, for older adults, practice was sufficient to have the learning effect partially generalize to three out of four tested untrained orientations that were close to the training orientation.

RT results for the untrained orientations (RO = $90^\circ$, $0^\circ$, and $67.5^\circ$) showed no training-based improvements (see results in Table S2 in Supplemental Materials). When RO was $22.5^\circ$, although the Age × Group × Time interaction was not significant ($F < 1$), the Group × Time interaction was significant, $F(1, 28) = 14.16$, $p = .001$, $\eta_p^2 = .34$. After splitting the data by age, the Group × Time interaction was still significant for both younger and older adults (younger: $F(1, 14) = 4.96$, $p = .043$, $\eta_p^2 = .26$; older: $F(1, 14) = 13.07$, $p = .003$, $\eta_p^2 = .48$). The older training group significantly reduced RTs through the training, $F(1, 9) = 26.95$, $p = .001$, $\eta_p^2 = .75$, whereas the older control group did not ($F < 1$). The younger training group significantly reduced RTs through the training, $F(1, 9) = 9.77$, $p = .012$, $\eta_p^2 = .52$, but the younger control group did not ($F < 1$). Reductions in mean RTs did not show age difference between the younger and older training group, $t(18) = -.025$, $p = .980$, $d = .01$.

Overall, for the threshold results, older adults (but not younger adults) showed significant transfer effects to the untrained orientation $0^\circ$ and the untrained orientations that were $22.5^\circ$. 
rotated from the training orientation (22.5° and 67.5°). For the RT results, both younger and older adults showed a small transfer effect of improvements in RTs to the untrained orientation 22.5°.

**Improvements on the visual working memory (VWM) task.** Data analyses for the VWM task performance were the same as in the original orientation discrimination task. For the orientation discrimination thresholds in the VWM task, we found a significant Age × Group × Time interaction, $F(1, 60) = 4.38$, $p = .041$, $\eta_p^2 = .07$, and a significant Group × Time interaction, $F(1, 60) = 15.63$, $p < .001$, $\eta_p^2 = .21$. After splitting the data by age, older adults showed a significant Group × Time interaction ($F(1, 30) = 16.48$, $p < .001$, $\eta_p^2 = .36$) and a significant main effect of time ($F(1, 30) = 14.52$, $p = .001$, $\eta_p^2 = .33$). The older training group showed significant training-related improvements of the thresholds, $F(1, 19) = 28.01$, $p < .001$, $\eta_p^2 = .60$, whereas the older control group did not, $F < 1$ (see Figure 4a). In contrast, younger adults did not show a significant Group × Time interaction ($F(1, 30) = 1.95$, $p = .173$, $\eta_p^2 = .06$), but showed a significant main effect of time ($F(1, 30) = 29.12$, $p < .001$, $\eta_p^2 = .49$). Both younger training and control groups significantly improved thresholds over time (training group: $F(1, 19) = 30.73$, $p < .001$, $\eta_p^2 = .62$; control group: $F(1, 11) = 6.41$, $p = .028$, $\eta_p^2 = .37$). These results suggest that the apparent improvements in the younger groups were largely due to practice effects. In addition, the older training group’s VWM thresholds after the training were comparable to the before-training thresholds of the younger training group, $t(38) = .75$, $p = .46$, $d = .01$. Therefore, whereas younger adults showed general practice-related improvements in the orientation discrimination thresholds, only those older adults who received the perceptual training, produced transfer effects to the VWM task.
For the RTs in the VWM task, none of the three-way interactions were significant ($F$s < 3.47, $ps > .07, \eta_p^2$s < .06), but the main effect of time was significant ($F(1, 60) = 12.49, p = .001, \eta_p^2 = .17$). As shown in Figure 4b, the main effect was primarily driven by reduced RTs for both younger and older training groups after the training, with no differences in reduction between them (as was indicated by the non-significant interactions).

**Discussion**

The present study examined age-related differences in perceptual learning on orientation discrimination. Furthermore, we aimed to determine whether the effect of perceptual learning can be transferred to untrained stimuli and subsequently improve VWM. A matching-to-sample task with high-contrast stimuli were used. Both younger and older adults received a three-day training session. Different from previous studies (e.g., Deloss et al., 2015), comparable control groups that received no training were also included.

Prior to the training, older adults showed age-related deficits in orientation discrimination. During training, both younger and older training groups revealed considerable improvements in both thresholds and RTs relative to their control groups. Older training participants improved their orientation discrimination thresholds and RTs in the same magnitude and learning rate as did younger training participants. Furthermore, older adults’ performance after training was the same as younger adults’ performance before training. Our perceptual training paradigm showed an improvement in performance for older adults that was transferred to the untrained orientations 22.5° and 67.5°, which were 22.5° rotated relative to the training orientation of 45°. Similar transfer effects were also observed for the untrained orientation 0°, which was 45° rotated from the training orientation. Furthermore, older adults were able to transfer perceptual learning in thresholds to the VWM task that was greater in cognitive loads than those in the training task. In
contrast, younger adults showed practice-based, but not training-based, improvements in the VWM task. These findings suggest that a perceptual training paradigm can be used to attenuate age-related declines in orientation discrimination. Also, these training effects can be generalized to other stimulus conditions and can help older adults overcome VWM capacity limitations.

At baseline, older adults showed higher orientation discrimination thresholds than younger adults, which is inconsistent with the finding of no age differences in Betts et al. (2007). Note that thresholds for both age groups in our study (younger $\approx 15^\circ$; older $\approx 21^\circ$) were greater than those in Betts et al. ($\approx 0.5^\circ$ for both younger and older). This suggests that our matching-to-sample task was more difficult than Betts et al.’s 1AFC task. For our task, participants had to make judgments based on a combination of multiple pieces of information: the order and orientations of two stimuli, and the orientation of the probe stimulus. These age differences in orientation discrimination thresholds could be the result of changes in sensory processing and/or working-memory capacity with age.

A major finding of the present study is that the perceptual training lowered orientation discrimination thresholds and RTs for both younger and older adults in similar magnitudes and learning rates. The current results from younger participants replicated the Deloss et al. (2015) study. Also, the results from older participants are consistent with previous findings with motion discrimination (Bower & Andersen, 2012) and contour integration (McKendrick & Battista, 2013). Taken together, older adults are able to produce similar perceptual learning effects to younger adults.

The present study did not show a significant Age $\times$ Group $\times$ Time interaction for the training orientation (although such 3-way interactions did occur for untrained orientations and for the VWM delayed task). This null finding for the training orientation is due to the use of low-
noise-level stimuli. The comparable learning for older adults was limited by the absence of a high-noise stimulus condition during the training (Deloss et al., 2014). Furthermore, these results extend previous findings on perceptual learning and show that perceptual training can improve orientation discrimination ability and speed up processing for both younger and older adults (Allen, Lien, Ruthruff, & Voss, 2014; Allen, Ruthruff, Elicker, & Lien, 2009; Bherer et al., 2005, 2006; Kramer, Larish, & Strayer, 1995, Matthews et al., 1999, 2001, Ratcliff, Thapar, & McKoon, 2006). The facilitation in performance could be due to a training-based decrease in the amount of information and cognitive resources required for decision-making. Together, our study provides evidence that even with a relatively short perceptual learning, it can attenuate age-related declines in orientation discrimination ability and potentially improve various perceptual functions of healthy older adults (Andersen et al., 2010; Bower, Watanabe, & Andersen, 2013; Deloss et al., 2014, 2015; McKendrick & Battista, 2013; Polat et al., 2012).

The second major finding in the present study is that older trainees showed a learning-based transfer effect in thresholds to untrained orientations that were 22.5° rotated from the training orientation. As hypothesized, learning effects are more likely to be transferred to untrained orientations that fall in the orientation tuning functions of training-target neurons (e.g., neurons that are tuned to orientations 12°–20° away from the training orientation, i.e., 22.5° and 67.5° in the present study). It is because neural representations of new orientations were similar enough to those of the training orientation. This result, together with Xu et al.’s (2012) finding, supports the notion of transfer of learning within the same feature channel (i.e., an orientation-tuning function).

In addition, older adults, but not younger adults, showed a particular improvement in thresholds at 0° that was 45° off the training orientation. This likely occurred because practice
for older adults induced changes in intermediate-level representations of visual processing (e.g., VWM processing). These changes in the intermediate-level visual processing may be a more general process that can transfer to other stimulus conditions. Another possibility is that the present task involved a fairly coarse orientation discrimination on low-level noise and high contrast stimuli. This task produced relatively higher mean orientation discrimination thresholds than previous studies (Betts et al., 2007). In younger adults, because the same improvement was not observed at the other three untrained orientations, the slight improvement in thresholds at one untrained orientation 67.5° indicates that perceptual learning was relatively specific to the training orientation (i.e., more difficult in transferring the improvements to untrained orientations). As for RT results, both younger and older adults showed faster responses at one of untrained orientations—22.5°. Because the same improvement was not observed at the other three untrained orientations, the apparent transfer of perceptual learning effects on RTs to the specific untrained orientation should not be over-interpreted.

In contrast to the specificity of perceptual learning observed in younger adults (which suggests an early neural locus of perceptual learning such as V1), our findings for older adults suggest that perceptual learning generalizes to intermediate-level representations of visual processing. This may provide an important clue for future investigations of the underlying mechanisms and generalization of perceptual learning in older adults.

The third major finding is that perceptual training produced a threshold improvement for older adults in the VWM task as compared to the control group. Previous studies have suggested that the transfer effect to the VWM task was due to a training-based perceptual enhancement (Berry et al., 2010) or an improvement in the allocation of attention (Mishra et al., 2015). Accordingly, similar performance enhancement should be observed for the younger training
group but not the younger control group. In contrast, we found that both younger training and control groups produced similar enhancement, suggesting that the improvement was due to practice in general. Therefore, their explanations cannot entirely account for the particular learning-based transfer effect on older adults in the present study. One possible explanation is that the limiting factor for orientation discrimination with a matching-to-sample task is not only perceptual processing but also a top-down control of VWM. Compared to younger adults, older adults may be more restricted in their abilities to exploit VWM using top-down control of perceptual processing (Wais & Gazzaley, 2014), but that training allows them to better utilize top-down control of attention (Lien, Ruthruff, & Kuhns, 2008; Madden, 2007). Another possibility is that both cognitive/inhibitory control (Braver, 2012) and training-based facilitation were delayed for older adults relative to younger adults—thereby allowing older adults to show the full potential of the facilitation at the longer (VWM) ISI.

One potential concern with the present matching-to-sample task is that participants simply encoded one of the two target stimuli on each trial, and that this unspecific strategy affected performance across training sessions. If our training outcomes were caused by an unspecific training strategy, then observed training effects should have transferred approximately equally across all untrained orientations. However, we found no learning effects for the 90° condition. Therefore, the improved performance over the 3-day training on the trained and untrained conditions was unlikely the result of learning the task by settling on the unspecific strategy.

Relative to the Berry et al. task (2010), the present perceptual training (using a more complex task) not only can improve perceptual performance for older adults, but also can act as a potential method to compensate for age-related declines in VWM (Anguera et al., 2013). Future
research that includes other manipulations of VWM (e.g., different ISIs; relevant or irrelevant distractions during the orientation discrimination task) is needed to determine whether older adults show any modulations of transfer effects by VWM demands.

**Conclusions**

The present study demonstrated that a three-day perceptual learning paradigm effectively improved perceptual performance for both younger and older adults. Older adults exhibited similar learning magnitudes and rates as younger adults did. These results were largely consistent with those obtained from recent aging studies on orientation training (Deloss et al., 2014, 2015) and attention training (e.g., Allen et al., 2014, 2009; Bherer et al., 2005, 2006; Kramer et al., 1995). One important note is that the training period of the present study is shorter than the Deloss et al. study (2015) and we included control groups whereas Deloss et al. did not. The notable findings of the present study are that perceptual learning improvements transferred to the untrained orientations that were 22.5° or 45° rotated from the training orientation, and the presence of transfer effects to VWM performance in older (but not younger) adults. Thus, our paradigm might be more generalizable in older adults than in younger adults. In summary, our study provides a potential framework for future research on cognitive training protocols designed to attenuate age-related declines in visual processing.
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Table 1

Means and standard deviations (in parentheses) of participants’ demographic information and results from perceptual and cognitive tests.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Younger Adults ($n = 32$)</th>
<th>Older Adults ($n = 32$)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Training ($n = 20$)</td>
<td>Control ($n = 12$)</td>
</tr>
<tr>
<td>Age (year)</td>
<td>22.3 (4.77)</td>
<td>22.8 (4.96)</td>
</tr>
<tr>
<td>Gender Ratio (F/M)</td>
<td>12/8</td>
<td>9/3</td>
</tr>
<tr>
<td>Years of Education</td>
<td>15.6 (2.50)</td>
<td>15.5 (2.24)</td>
</tr>
<tr>
<td>Visual Acuity$^a$</td>
<td>20/20.2 (0.05)</td>
<td>20/20 (0)</td>
</tr>
<tr>
<td>Digit Symbol$^b$</td>
<td>82.3 (13.25)</td>
<td>83.3 (10.87)</td>
</tr>
<tr>
<td>Vocabulary$^c$</td>
<td>15.8 (3.02)</td>
<td>16.2 (4.95)</td>
</tr>
</tbody>
</table>

Note. F/M = Female/Male.

$^a$Visual acuity was measured using the Snellen chart. $^b$Digit Symbol Substitution Test (Wechsler, 1981). $^c$Mill Hills Vocabulary Test (Raven, Raven, & Court, 1998).
Table 2

*Results of the assessment of the perceptual-learning-based training effects on mean orientation discrimination thresholds and mean RTs for the training orientation (RO = 45°).*

<table>
<thead>
<tr>
<th></th>
<th>Thresholds</th>
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<th>RTs</th>
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<td></td>
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<td>Thresholds</td>
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<td>RTs</td>
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<tr>
<td>Three-Way ANOVA a</td>
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<td></td>
</tr>
<tr>
<td>Age × Group × Time</td>
<td>1.217</td>
<td>.274</td>
<td>.020</td>
<td>.352</td>
</tr>
<tr>
<td>Group × Time</td>
<td>37.645</td>
<td>&lt; .001</td>
<td>.386</td>
<td>16.382</td>
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<tr>
<td>Age × Time</td>
<td>.254</td>
<td>.616</td>
<td>.004</td>
<td>.334</td>
</tr>
<tr>
<td>Time</td>
<td>87.243</td>
<td>&lt; .001</td>
<td>.593</td>
<td>22.655</td>
</tr>
<tr>
<td>Two-Way ANOVA b</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Younger Adults b</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Group × Time</td>
<td>12.195</td>
<td>.002</td>
<td>.289</td>
<td>5.198</td>
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<tr>
<td>Time</td>
<td>37.603</td>
<td>&lt; .001</td>
<td>.556</td>
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<td>Older Adults b</td>
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<td></td>
<td></td>
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<tr>
<td>Group × Time</td>
<td>27.244</td>
<td>&lt; .001</td>
<td>.476</td>
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<td>Time</td>
<td>50.383</td>
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<td>.627</td>
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*Note.* $p < .05$. The significant $p$ values are bolded.

aThe three-way Age × Group × Time ANOVA, $df_1 = 1$, $df_2 = 60$ (i.e. $F(1, 60)$). bThe two-way Group × Time ANOVA for either younger or older age group after splitting the data by age group, $df_1 = 1$, $df_2 = 30$ (i.e. $F(1, 30)$).
Table 3

*Results of the assessment of the perceptual-learning-based transfer effects on mean orientation discrimination thresholds for the untrained orientations (RO = 0°, 22.5°, and 67.5°) based on the combined dataset.*

<table>
<thead>
<tr>
<th></th>
<th>RO = 0°</th>
<th></th>
<th>RO = 22.5°</th>
<th></th>
<th>RO = 67.5°</th>
<th></th>
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</thead>
<tbody>
<tr>
<td></td>
<td>$F$</td>
<td>$p$</td>
<td>$\eta^2$</td>
<td>$F$</td>
<td>$p$</td>
<td>$\eta^2$</td>
</tr>
<tr>
<td>Three-Way ANOVAa</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age × Group × Time</td>
<td>5.829</td>
<td>&lt;.05</td>
<td>.172</td>
<td>4.045</td>
<td>.054</td>
<td>.126</td>
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<tr>
<td>Group × Time</td>
<td>6.776</td>
<td>&lt;.05</td>
<td>.195</td>
<td>4.273</td>
<td>.048</td>
<td>.132</td>
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<tr>
<td>Age × Time</td>
<td>.427</td>
<td>&gt;.05</td>
<td>.015</td>
<td>.199</td>
<td>.659</td>
<td>.007</td>
</tr>
<tr>
<td>Time</td>
<td>.711</td>
<td>&gt;.05</td>
<td>.025</td>
<td>16.238</td>
<td>&lt;.001</td>
<td>.367</td>
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<tr>
<td>Two-Way ANOVAb</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Younger Adultsb</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Group × Time</td>
<td>.097</td>
<td>&gt;.05</td>
<td>.007</td>
<td>.002</td>
<td>.964</td>
<td>&lt;.001</td>
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<tr>
<td>Time</td>
<td>.098</td>
<td>&gt;.05</td>
<td>.007</td>
<td>8.469</td>
<td>.011</td>
<td>.377</td>
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<tr>
<td>Older Adultsb</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Group × Time</td>
<td>6.931</td>
<td>&lt;.05</td>
<td>.331</td>
<td>6.697</td>
<td>.021</td>
<td>.324</td>
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<tr>
<td>Time</td>
<td>.616</td>
<td>&gt;.05</td>
<td>.042</td>
<td>8.066</td>
<td>.013</td>
<td>.366</td>
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</table>

*Note.* $p < .05$. The significant $p$ values are bolded.

aThe three-way Age × Group × Time ANOVA, $df_1 = 1, df_2 = 28$ (i.e. $F(1, 28)$). bThe two-way Group × Time ANOVA for either younger or older age group after splitting the data by age group, $df_1 = 1, df_2 = 14$ (i.e. $F(1, 14)$).
Figure 1. a. Illustration of the temporal sequence of stimulus presentation for the orientation discrimination task. b. Two grating stimuli (GSs) and the probe presented in a training trial. Left: a GS with the reference orientation (RO = 45°) and the other GS with an orientation tilted counter-clockwise relative to the reference orientation (RO + ΔO; in the example shown, ΔO = 22.5°); Right: the probe GS that contained either RO or RO + ΔO. c. GSs at the untrained orientations: 67.5° (upper left), 22.5° (upper right), 0° (lower left), and 90° (lower right).
Figure 2. Effects of perceptual learning on the orientation discrimination task in which the reference orientation was 45°. Data are shown as a function of group (training and control) and age (younger and older): training_YA = younger training group; control_YA = younger control group; training_OA = older training group; and control_OA = older control group. 

a. Mean orientation discrimination thresholds before and after the three-day training; b. Mean orientation discrimination thresholds across five daily sessions (each symbol represented daily mean thresholds averaged on all the participants within each group); c. Mean reaction times (RTs) before and after the training sessions; d. Mean RTs across five daily sessions (each symbol
represented daily mean RTs averaged on all the participants within each group). Error bars represent ±1 standard error of the mean. In panels a and c, asterisks indicate significant differences ($p < .05$) between relevant conditions.
Figure 3.
Figure 3. Effects of perceptual learning on untrained orientations. Data are shown as a function of group (training and control) and age (younger and older): training_YA = younger training group; control_YA = younger control group; training_OA = older training group; and control_OA = older control group. **a.** Mean orientation discrimination thresholds on 22.5° before and after the three-day training; **b.** Mean orientation discrimination thresholds on 67.5° before and after the three-day training; **c.** Mean orientation discrimination thresholds on 0° before and after the three-day training; **d.** Mean orientation discrimination thresholds on 90° before and after the three-day training. Error bars represent ±1 standard error of the mean. Asterisks indicate significant differences ($p < .05$) between relevant conditions.
Figure 4. Performance on the longer-delay-time visual working memory (VWM) task before and after the training. Data are shown as a function of group (training and control) and age (younger and older): training_YA = younger training group; control_YA = younger control group; training_OA = older training group; and control_OA = older control group. a. Mean orientation discrimination thresholds before and after the three-day training; b. Mean RTs before and after the training sessions. Error bars represent ±1 standard error of the mean. Asterisks indicate significant differences ($p < .05$) between relevant conditions.