A new format of perceptual learning based on evidence abstraction from multiple stimuli

Xin-Yu Xie

School of Psychology, IDG/McGovern Institute for Brain Research at Peking University, and Center for Life Sciences, Peking University, Beijing, China

Cong Yu

School of Psychology, IDG/McGovern Institute for Brain Research at Peking University, and Center for Life Sciences, Peking University, Beijing, China

Perceptual learning, which improves stimulus discrimination, typically results from training with a single stimulus condition. Two major learning mechanisms, early cortical neural plasticity and response reweighting, have been proposed. Here we report a new format of perceptual learning that by design may have bypassed these mechanisms. Instead, it is more likely based on abstracted stimulus evidence from multiple stimulus conditions. Specifically, we had observers practice orientation discrimination with Gabors or symmetric dot patterns at up to 47 random or rotating location × orientation conditions. Although each condition received sparse trials (12 trials/session), the practice produced significant orientation learning. Learning also transferred to a Gabor at a single untrained condition with two- to three-times lower orientation thresholds. Moreover, practicing a single stimulus condition with matched trial frequency (12 trials/session) failed to produce significant learning. These results suggest that learning with multiple stimulus conditions may not come from early cortical plasticity or response reweighting with each particular condition. Rather, it may materialize through a new format of perceptual learning, in which orientation evidence invariant to particular orientations and locations is first abstracted from multiple stimulus conditions and then reweighted by later learning mechanisms. The coarse-to-fine transfer of orientation learning from multiple Gabors or symmetric dot patterns to a single Gabor also suggest the involvement of orientation concept learning by the learning mechanisms.

Introduction

Training improves the sensitivity of humans to fine differences of basic visual features. Typically, these perceptual learning experiments are performed with a specific stimulus condition (e.g., a specific orientation or retinal location), and learning is often specific to this condition. The specificity has prompted many perceptual learning researchers to propose that the observed sensitivity improvements may result from tuning changes in early visual neurons (Karni & Sagi, 1991; Schoups, Vogels, & Orban, 1995; Teich & Qian, 2003) or reweighting of the responses of these neurons that respond to the specific stimulus condition (Mollon & Danilova, 1996; Dosher & Lu, 1998, 1999; Yu, Klein, & Levi, 2004; Dosher, Jeter, Liu, & Lu, 2013). More recent evidence indicates that even specific perceptual learning can be rendered significantly and often completely transferrable to new stimulus conditions with double training (Xiao et al., 2008; Zhang et al., 2010; Zhang, Cong, Klein, Levi, & Yu, 2014; Wang et al., 2016; Xiong, Zhang, & Yu, 2016), prevention of stimulus adaption (Harris, Gliksberg, & Sagi, 2012), or covert attention to the trained stimuli (Donovan, Szpiro, & Carrasco, 2015). It is thus unlikely that learning is limited to sensory neurons directly activated by the training stimuli or reweighting of the responses of these neurons. Rather, more general rules for response reweighting may have been abstracted through reweighting responses to a specific stimulus, so that perceptual learning is transferrable in principle (Xiao et al., 2008; Zhang et al., 2010; Wang et al., 2016).

Here we present evidence for a new format of perceptual learning that by design may bypass the above early plasticity or response reweighting mechanisms of learning. Our observers practiced orientation discrimination of a Gabor stimulus at 12 locations and 4 orientations. The stimulus location and orientation were changed from trial to trial, but one location/orientation combination served as the pre-/post-training condition and was skipped; therefore, there were 47 training conditions and

1 pre-/post-training test condition. During training, each condition was repeated twice per block of trials, for a total of 12 trials per daily session. The repeats of the same condition were separated by 4 to 5 minutes, on average, within a session. The purpose of having very sparse trials with very long time gaps for each training condition was to prevent learning if each training condition was practiced alone. Therefore, significant perceptual learning with multiple stimulus conditions would suggest that the learning is less likely based on early neural plasticity or response reweighting associated with each particular condition. Rather, it more likely occurs on the basis of abstracted evidence from multiple stimulus conditions that are not specific to particular stimulus orientations and locations.

Methods

Observers and apparatus

Sixty-eight observers (17–28 years old; 32 males and 36 females) with normal or corrected-to-normal vision were recruited from undergraduate and graduate students. They were new to psychophysical experiments and were naïve to the purposes of the study. The experiments were approved by the Peking University institutional review board. Informed written consent was obtained before data collection from each observer. This work was carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

The stimuli were generated with Psychtoolbox-3 ([Pelli, 1997](#)) and presented on a 21-in. CRT monitor (1024 × 768 pixels; pixel size, 0.39 × 0.39 mm; 120-Hz frame rate; 46.0 cd/m^2 mean luminance). The screen luminance was linearized by an 8-bit look-up table. Viewing was binocular at a distance of 1 m, and a chin and head rest stabilized the head. Viewing was through a circular opening (diameter = 17°) in black cardboard that covered the rest of the monitor screen. Experiments were run in a dimly lit room. An EyeLink-1000 eye tracker (SR Research, Kanata, Ontario, Canada) monitored eye movements. A trial where the eye position deviated from the fixation point for >2° would be immediately aborted and later repeated. The mean deviation from the fixation across all trials in all observers was 0.71°, and the mean of individual standard deviations was 0.36°; therefore, our data were not significantly affected by improper eye movements.

Stimuli, tasks, and procedures

The stimuli included Gabor gratings (Gaussian-windowed sinusoidal grating) and symmetric dot patterns. The Gabor stimulus was 3 cpd in spatial frequency, 47% in contrast, 0.68° in standard deviation, and random in phase for every presentation. A symmetric dot pattern consisted of 18 pairs of bilaterally symmetric white dots (0.1° diameter), which were confined to an area divided into 18 × 18 invisible square compartments (0.16° × 0.16° each). The placement of the 18 dots on one side of the symmetry axis (within 18 rows by 9 columns of available compartments) was subject to the following constraints: (1) no dot was placed in the column of compartments nearest to the symmetry axis; (2) for the other 8 columns, 2 of them were randomly chosen to hold 3 dots in each column, and each of the remaining 6 columns contained 2 dots; (3) only one dot was allowed in each of the 18 rows by randomly assigning row numbers to the 18 dots on one side of the symmetric pattern; and (4) the location of each dot was randomly jittered by 0° to 0.04° from the compartment center. After positioning the 18 dots on one side of the symmetry axis, the whole symmetric pattern was generated by placing 18 mirror-imaged dots on the other side. The dot pattern was regenerated for each stimulus presentation. A Gabor or symmetric dot pattern was presented on a mean luminance screen background at 5° retinal eccentricity.

The orientation discrimination threshold was measured with a two-interval, forced-choice staircase procedure. In each trial, a small fixation cross preceded the first interval by 500 ms and stayed throughout the trial. The stimuli at the reference orientation and the test orientation (reference + Δori) were shown in two 100-ms (for a Gabor) or 200-ms (for a dot pattern) stimulus intervals, respectively, in a random order. The two stimulus intervals were separated by a 500-ms interstimulus interval. The observers judged which stimulus interval contained the more clockwise-oriented stimulus. In addition, the contrast discrimination threshold (for Gabor only) was measured with a similar procedure, except that the stimulus contrast was varied (reference + Δcontrast). The observers judged which interval had higher contrast. Auditory feedback was given on incorrect responses in both orientation and contrast discrimination tasks.

Thresholds were estimated following a three-down/one-up staircase rule that converged at a 79.4% correct response rate. The step size of the staircase was 0.05 log units. For pre-/post-training testing, each staircase consisted of four preliminary reversals and six experimental reversals (approximately 50–60 trials). The geometric mean of the experimental reversals was taken as the threshold for each staircase run. During training with multiple random or rotating conditions (see Training designs, below), a single staircase varied the orientation or contrast difference for all stimulus conditions through 94 trials (two for each condition). The number of training trials with the baseline group
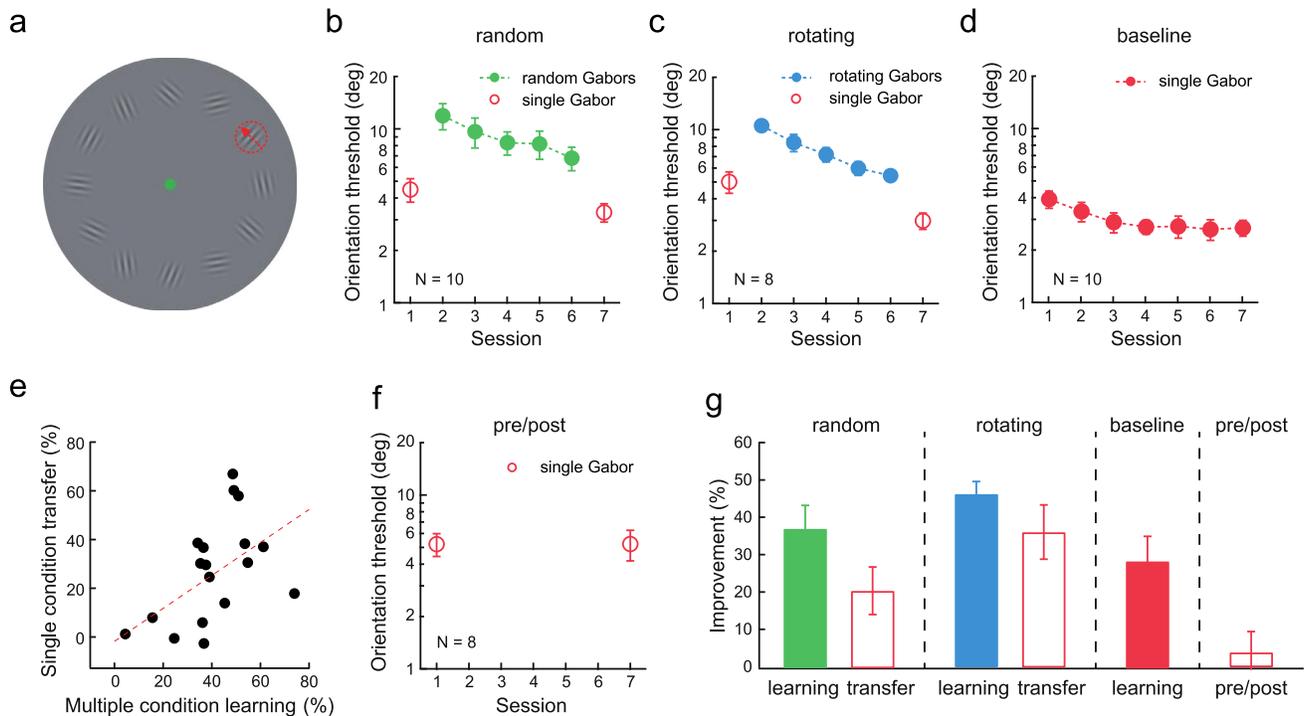
Figure 1. Perceptual learning of orientation discrimination with a location- and orientation-changing Gabor stimulus. (a) A Gabor stimulus varied at 47 location/orientation conditions trial by trial during training. The red circle and arrow indicate the pre-/post-training stimulus location/orientation that was skipped during training. (b) The session-by-session threshold changes with the random Gabor over 47 stimulus conditions during training, as well as the pre-/post-training thresholds at an untrained condition. (c) The same as (b) except that the Gabor rotated in location and orientation during training. (d) The threshold changes in the baseline condition in which training and pre-/post-training testing were performed with the same stimulus condition. (e) A comparison of the transfer and learning effects. The dashed line shows linear regression. (f) The pretest effects; this control group completed the same pre- and post-tests but skipped the training sessions. (g) A summary of learning (and transfer when applicable) with different groups of observers. Error bars indicate ±1 standard error of the mean.

was equal to the total number of training trials for the groups with multiple stimulus conditions. The geometric mean of the last six reversals was taken as the threshold for each staircase run. A pre- or post-training testing session consisted of five staircases. The training consisted of five daily sessions, each consisting of six staircases. Each session lasted approximately 1 hour.

Training designs

During multiple stimulus condition training, a Gabor varied at 12 equally spaced locations (2.6 arcdeg apart) and 4 equally spaced reference orientations (45° apart: 20°, 65°, 110°, and 155°) (Figure 1a). The orders of stimulus presentation were different between two multiple-condition training groups. For observers in the random group, the stimulus location and reference orientation were randomized from trial to trial, but, for those in the rotating group, the stimulus location rotated in a counterclockwise order, and the reference orientation rotated in a clockwise order. There were 47 training conditions and one pre-/post-training

condition that was skipped during training. For a third baseline group, the training condition was the same as the pre-/post-training condition, whereas the number of training trials was the same as those in the random and rotating groups. The pre-/post-training location/orientation for each observer in the random, rotating, and baseline groups was randomly chosen from four location/orientation conditions, which were a combination of two reference orientations at 20° and 110° (to avoid oblique effects), and two locations at the 1-o'clock position and the 7-o'clock position. The pre-/post-training conditions were roughly matched among groups. Multiple-condition training with symmetric dot patterns was also performed, along with a number of control conditions, which are detailed in the Results section.

Sample size and statistical analysis

Our previous studies indicated that when data from two or three experiments are compared, a sample size of eight observers is sufficient to produce strong effect

sizes (Xiong et al., 2016; Xiong, Tan, Zhang, & Yu, 2019). We basically followed this rule of thumb to determine the sample size (8 to 10 in all experiments).

Data were analyzed with SPSS Statistics 20.0 (IBM, Armonk, NY). The learning effects were measured by the percent threshold improvements from pre- to post-test session or from first to fifth training session. One-way analysis of variance (ANOVA) and *t*-tests were used to analyze the threshold improvements. The statistical powers were measured with Cohen's *d* in *t*-tests and partial eta-squared in ANOVA.

Results

We were interested in two learning effects: first and in particular, whether training with multiple stimulus conditions would generate significant learning; and second, whether such learning could transfer to the untrained pre-/post-training condition, and how much the transfer would be when compared to the baseline group that practiced the pre-/post-training condition directly.

The first learning effect for the multiple stimulus conditions was calculated as the percent threshold improvement from the first to the fifth (last) training session (Figures 1b and 1c). For the random group ($n = 10$), the stimulus location and orientation were randomized from trial to trial. The orientation thresholds with multiple stimulus conditions were about three times as high as the pre-/post-training condition that contained a single stimulus, and training reduced the thresholds with multiple stimulus conditions by $37.0 \pm 6.2\%$ ($t_9 = 5.93$; $p < 0.001$; 95% confidence interval [CI], 22.9–51.1; Cohen's $d = 1.87$; two-tailed paired *t*-test here and in later analyses unless otherwise specified) (Figures 1b and 1g). We suspected that the higher thresholds might have resulted from increased stimulus uncertainty due to stimulus randomization. Therefore, we had the rotating group ($n = 8$) practice the same stimuli while the stimulus location and orientation were rotated. Such orderly stimulus presentations would reduce stimulus uncertainty and facilitate learning (Kuai, Zhang, Klein, Levi, & Yu, 2005; Zhang et al., 2008). However, the orientation thresholds with rotating conditions were also more than twice as high as those with the pre-/post-training condition, indicating that the high thresholds were not much related to stimulus uncertainty. Training reduced orientation thresholds with rotating conditions by $46.0 \pm 3.3\%$ ($t_7 = 13.74$; $p < 0.0001$; 95% CI, 38.1–53.9; Cohen's $d = 4.86$) (Figures 1c and 1g). There was no significant difference for learning between the random and rotating groups ($t_{16} = 1.17$; $p = 0.259$; 95% CI, –7.2 to 25.1; Cohen's $d = 0.58$; two-tailed independent *t*-test). These

results indicate that our observers were able to learn orientation discrimination with changing stimulus locations and orientations, regardless of whether the stimuli were presented in random or rotating orders.

The second learning effect, or the transfer effect at the untrained pre-/post-training condition, was calculated as the percent threshold improvement from the pre- to the post-training session. As mentioned earlier, the pre-training orientation thresholds with multiple random or rotating stimulus conditions were two to three times as high as those with the single stimulus pre-/post-training condition. Nevertheless, training with multiple stimulus conditions improved orientation thresholds at the untrained pre-/post-training condition by $20.6 \pm 6.3\%$ ($t_9 = 3.27$; $p = 0.010$; 95% CI, 6.3–34.8; Cohen's $d = 1.03$) for the random group (Figure 1b) and by $36.0 \pm 7.2\%$ ($t_7 = 5.03$; $p = 0.002$; 95% CI, 19.1–53.0; Cohen's $d = 1.78$) for the rotating group (Figure 1c). The orientation thresholds for the baseline group ($n = 10$), which used the same single condition for training and pre-/post-training testing, improved by $28.5 \pm 6.6\%$ ($t_9 = 4.35$; $p = 0.002$; 95% CI, 13.6–43.3; Cohen's $d = 1.37$) (Figures 1d and 1g). One-way ANOVA found no significant difference of improvements among the three groups ($F(2, 25) = 1.29$; $p = 0.293$; $\eta^2 = 0.094$).

Moreover, we found that the learning effects with multiple-condition training and the transfer effects at the untrained pre-/post-training condition were positively correlated (Figure 1e). Pearson $r = 0.50$ ($p = 0.037$) when data from the random and rotating groups were pooled for analysis. Therefore, orientation learning with multiple stimulus conditions transferred to an untrained single stimulus condition, with more learning leading to more transfer.

We also had a control group of observers ($n = 8$) repeat the same pre-/post-test sessions but skip the training sessions to measure the pretest effects. The orientation thresholds were changed by merely $4.0 \pm 5.5\%$ ($t_7 = 0.73$; $p = 0.491$; 95% CI, –9.0 to 17.0; Cohen's $d = 0.26$) (Figure 1f). Therefore, the learning transfer to the untrained pre-/post-training conditions from orientation learning with multiple conditions (Figures 1b and 1c) could not be completely accounted for by the pretest effects.

Another control experiment ruled out two more alternative explanations of the above learning effects with multiple location/orientation conditions: First, the learning effects could be task unspecific in the visual periphery. Second, even the sparse trials at a single training condition were sufficient to produce learning. In the experiment, observers practiced contrast discrimination instead of orientation discrimination, with a Gabor stimulus rotating in locations and orientations. Moreover, instead of skipping the pre-/post-training test condition, the observers were
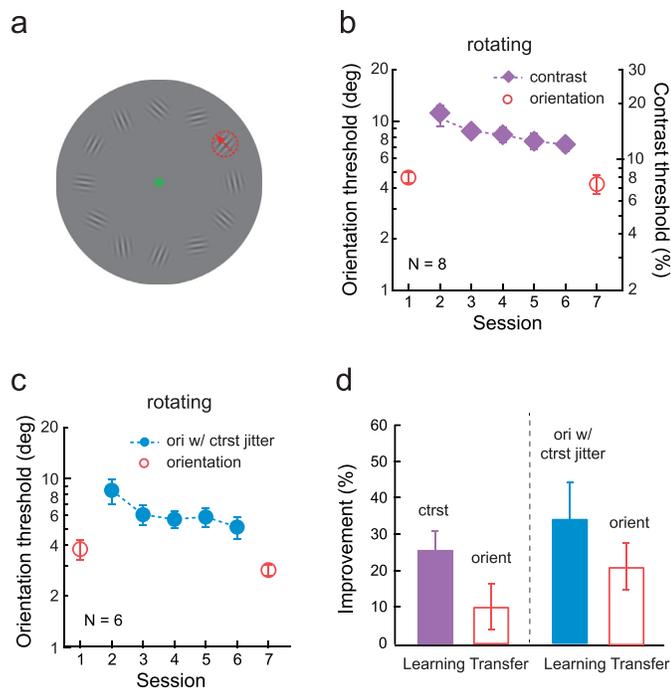
Figure 2. The control experiment for the effects of task unspecific learning and sparse training at a single condition. (a) The observers practiced contrast discrimination with a Gabor stimulus rotating at 47 training conditions. They also performed orientation discrimination at one condition, indicated by the red circle and arrow, when the Gabor rotated to it, as well as in pre-/post-training testing. (b) The session-by-session contrast threshold changes with the rotating Gabor (right *y*-coordinate), as well as the pre-/post-training orientation thresholds at a single sparsely orientation trained condition (left *y*-coordinate). (c) Control of the control; the session-by-session orientation threshold changes with the rotating Gabor over 47 stimulus conditions during training while the contrast of the Gabor was jittered, as well as the pre-/post-training thresholds at an untrained condition. (d) Summary of learning and transfer effects in (b) and (c). Error bars indicate ±1 standard error of the mean.

pre-cued to perform orientation discrimination when the Gabor rotated to this condition (2 trials per staircase and 12 trials per daily session) (Figure 2a).

Training reduced contrast thresholds by $25.9 \pm 5.0\%$ ($t_7 = 5.15$; $p = 0.001$; 95% CI, 14.0–37.8; Cohen's $d = 1.82$) (Figures 2b and 2d); therefore, the observers could also learn contrast discrimination with multiple location/orientation conditions. However, the orientation thresholds were not significantly changed for the sparsely orientation trained and pre-/post-training tested condition ($10.4 \pm 6.3\%$; $t_7 = 1.66$; $p = 0.142$; 95% CI, –4.5 to 25.3; Cohen's $d = 0.59$). Here the changes of orientation thresholds showed large individual differences, probably reflecting various degrees of general task-unspecific learning in

individual observers. However, the orientation threshold changes were significantly less than the transfer effects from orientation learning of the same rotating stimuli in Figure 1c ($10.4 \pm 6.3\%$ vs. $36.0 \pm 7.2\%$; $t_{14} = 2.68$; $p = 0.018$; 95% CI, 5.1–46.0; Cohen's $d = 1.34$), but were similar to the pretest effects in Figure 1f ($10.4 \pm 6.3\%$ vs. $4.0 \pm 5.5\%$; $t_{14} = 0.77$; $p = 0.455$; 95% CI, –11.5 to 24.3; Cohen's $d = 0.38$). Therefore, the observed multiple stimulus orientation learning (Figures 1b and 1c) could not be fully accounted for by general learning. Moreover, practice with sparse trials at a single training condition alone was insufficient to produce learning at that particular condition.

There was a concern that the contrast-varying stimuli per se could prevent orientation learning, which would invalidate the above control (Figure 2b). To address this issue, we ran a control of the control by having six new observers repeat the multiple-condition orientation learning experiment in Figure 1c, but with the stimulus contrast varied. Specifically, the observers practiced 47 rotating orientation/location conditions while the contrast of the Gabor was jittered ±1.2 times the average contrast thresholds in the first training session (Figure 2b). Training improved the orientation thresholds with 47 stimulus conditions by $34.2 \pm 9.8\%$ ($t_5 = 3.48$; $p = 0.018$; 95% CI, 8.9–59.5; Cohen's $d = 1.42$) and the untrained pre-/post-training condition by $21.5 \pm 6.4\%$ ($t_5 = 3.35$; $p = 0.020$; 95% CI, 5.0–37.9; Cohen's $d = 1.37$) (Figures 2c and 2d). These data therefore validated the above control experiment with contrast-varying stimuli.

In earlier experiments (Figure 1), the stimulus varied at 12 equally spaced locations. The center-to-center distance between two adjacent locations was 2.6 arcdeg. There was a chance that some V1 neurons with larger receptive fields could integrate stimulus evidence from adjacent locations to facilitate learning. To minimize this possibility, in a third control experiment we reduced the stimulus locations in Figure 1a by half to increase the center-to-center distance to 5 arcdeg, with all other stimulus parameters remaining unchanged (Figure 3a). There were now six Gabor locations and four Gabor orientations, for a total of 24 combined location/orientation conditions. The Gabor stimulus randomized among 23 training conditions but skipped the 24th pre-/post-training condition. The observers practiced orientation discrimination at each training condition with the same number of trials (2 trials per staircase and 12 trials per daily session) as before.

Training improved orientation discrimination with the random Gabor by $17.9 \pm 7.6\%$ ($t_8 = 2.35$; $p = 0.047$; 95% CI, 0.3–35.6; Cohen's $d = 0.78$) (Figures 3b and 3c; the six-location Gabor learning condition). In the earlier 12-location condition (Figure 1b), training with the same number of trials (2.5 training sessions) improved orientation thresholds with the random Gabor by $22.4 \pm 7.1\%$ ($t_9 = 3.16$; $p = 0.012$; 95% CI,
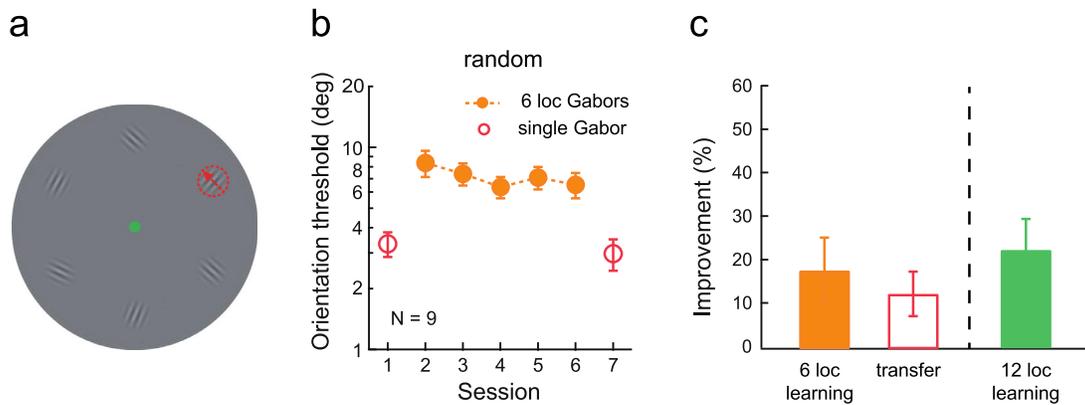
Figure 3. Orientation learning with the Gabor randomized at six locations. (a) A Gabor stimulus randomly varied among 23 location/orientation conditions trial by trial during training. The red circle and arrow indicate the pre-/post-training testing location and orientation where no training was performed. (b) The session-by-session threshold changes with the random Gabor, as well as the pre-/post-training thresholds at the untrained condition. (c) A summary of orientation learning with the random Gabor at six locations and its transfer to an untrained pre-/post-training condition, as well as orientation learning with matched number of trials from the earlier 12-location training condition. Error bars indicate ±1 standard error of the mean.

6.4–38.4; Cohen's $d = 1.00$) (Figure 3c; 12-location learning condition). The improvements with matched numbers of trials in two training conditions were similar ($t_{17} = 0.43$; $p = 0.677$; 95% CI, –17.5 to 26.4; Cohen's $d = 0.20$) (Figure 3c; six-location vs. 12-location learning conditions). These results showed that the observers could learn orientation discrimination with multiple stimulus conditions when the inter-stimulus distance was nearly doubled to further reduce possible spatial integration of stimulus evidence by V1 neurons having relatively large receptive fields. Instead, the amount of learning was dependent on the accumulation of stimulus evidence (or the number of training trials) from multiple training conditions. In addition, the learning also transferred to the pre-/post-training condition ($12.6 \pm 5.2\%$; $t_8 = 2.42$; $p = 0.042$; 95% CI, 0.6–24.6; Cohen's $d = 0.81$) (Figures 3b and 3c; single Gabor transfer condition).

Previously, we showed that orientation learning from single-condition training can transfer between symmetric dot patterns and Gabor gratings that are physically distinct (Wang et al., 2016). Here we tested whether training with multiple symmetric dot patterns could also improve orientation discrimination and whether learning could transfer to a Gabor grating.

Nine new observers practiced orientation discrimination with the symmetry axis of the dot pattern, with the axis rotating trial by trial at 47 location/orientation conditions (Figure 4a) in a manner identical to that with the previous rotating Gabor training conditions (Figure 1c). Before and after training, orientation thresholds with the Gabor grating were measured at the untrained condition. Training improved orientation thresholds with the rotating symmetry axis by $33.1 \pm 6.1\%$ ($t_8 = 5.47$; $p = 0.001$; 95% CI, 19.1–47.1; Cohen's $d = 1.82$)

(Figures 4b and 4c), again demonstrating orientation learning with multiple stimulus conditions when the trials for each condition were sparse. It also improved Gabor orientation discrimination at the untrained pre-/post-training condition by $25.5 \pm 6.1\%$ ($t_8 = 4.16$; $p = 0.003$; 95% CI, 11.4–39.7; Cohen's $d = 1.39$) (Figures 4b and 4c). The learning and transfer effects were also positively correlated ($r = 0.765$; $p = 0.016$) (Figure 4d). This transfer of orientation learning from symmetry axis to grating, as well as the correlation between the learning and transfer effects, indicated that the stimulus physical properties were also detached from current orientation learning, consistent with our proposal that perceptual learning at its core is concept learning (e.g., improving the conceptual representation of orientation) (Wang et al., 2016).

Discussion

In this study, we demonstrated evidence for a new format of perceptual learning. Superficially, what makes this new format of learning unique is the extreme experimental design. The observers practice as many as 47 stimulus conditions, each of which is repeated sparsely with long time gaps (4–5 min), and yet significant learning is evident. Fundamentally, learning with the current experimental design could bypass the hypothesized early cortical plasticity and response reweighting mechanisms that are specific to the trained stimuli. Because practicing a single Gabor condition with matched trial frequency failed to produce significant learning (Figure 2), learning with multiple stimulus conditions is less likely based on early cortical plasticity or response reweighting associated
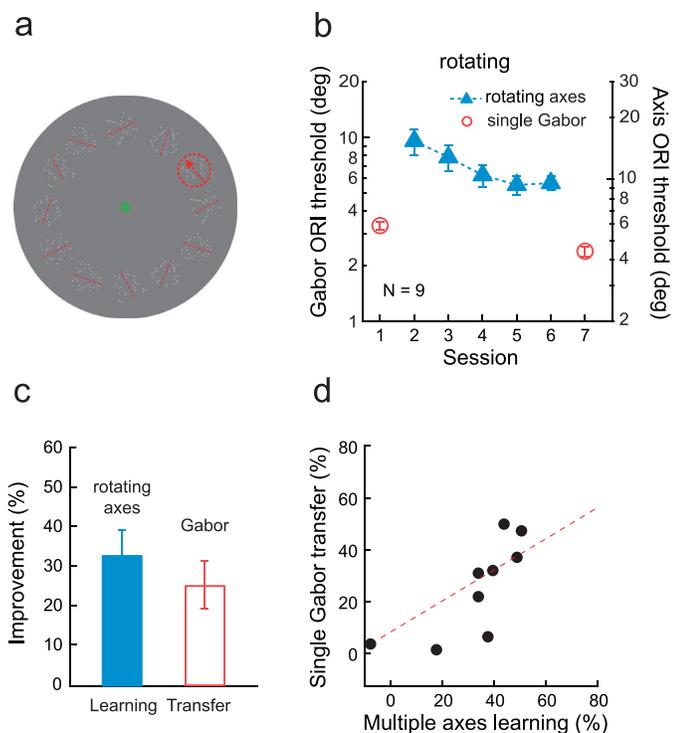
Figure 4. Perceptual learning of orientation discrimination with rotating symmetry axis. (a) Symmetric dot patterns with their axes rotated in location and orientation among 47 training conditions trial by trial. Each dashed red line indicates the invisible symmetry axis of a dot pattern. The red circle and arrow represent the location and orientation of a Gabor stimulus used only in pre-/post-training measurements. (b) The session-by-session threshold changes with the rotating symmetry axis (right *y*-coordinate), as well as the pre-/post-training thresholds with the Gabor at an untrained condition (left *y*-coordinate). (c) A summary of orientation learning with the rotating symmetry axis and its transfer to Gabor orientation discrimination at the untrained condition. (d) A comparison of the learning effects with symmetric dot patterns and transfer effects with a Gabor. The dashed line shows linear regression. Error bars indicate ±1 standard error of the mean.

with each particular condition. Rather, some high-level processes may abstract stimulus evidence from multiple stimulus conditions (i.e., taking orientation inputs with particular orientation and location information discarded) before reweighting can take place to produce learning.

What characterizes the new format of perceptual learning is probably the greatly elevated thresholds with multiple stimulus conditions that are two to three times as high as those with the single stimulus condition (Figure 1). This suggests that the abstracted orientation evidence from multiple stimulus conditions may be more coarsely represented at some higher visual areas such as V4. V4 neurons

have larger receptive fields and poorer orientation tuning than V1 neurons, so orientation evidence represented by V4 would lead to higher orientation discrimination thresholds. Indeed, neurophysiological evidence has suggested the involvement of V4 in orientation discrimination learning (Yang & Maunsell, 2004; Raiguel, Vogels, Mysore, & Orban, 2006). Another prominent characteristic in the new learning format is that the coarse orientation learning with multiple stimulus conditions still transfers to fine orientation representation with the single Gabor at the pre-/post-training condition (Figure 1), even from multiple symmetric dot patterns to a single Gabor (Figure 4). This transfer may be attributed to a third, conceptual representation of orientation. As we proposed previously, perceptual learning can operate at a conceptual level, so that learning is transferrable to stimuli defined by distinct physical properties and discriminated at different precisions or thresholds (Wang et al., 2016).

To account for the frequently observed transfer of perceptual learning to untrained retinal locations, Dosher et al. (2013) updated their reweighting model by adding a higher level, location-unspecific representation of the stimulus feature on top of the original location-specific representation and simultaneously modeling learning (reweighting) at both representations. In this context, our multiple-condition training design limits learning to the higher level stimulus representation while bypassing the low-level stimulus representation.

Our results may also provide important constraints to a future version of the integrated reweighting model. First, the model may need to allow learning transfer across orientations, as demonstrated in our previous double-training studies (Zhang et al., 2010; Xiong et al., 2016). Dosher et al. (2013) emphasized that the model predicts strict orientation specificity, which is inconsistent with the existing orientation transfer results. Second, the model may need to allow learning at a higher level stimulus representation to transfer completely to a low-level stimulus representation, as Figure 1 indicates. Third, the model may need to allow learning transfer between stimuli, such as the Gabor gratings and random dot patterns used in this study, that are physically different, are based on different neural encoders, and have different levels of precision (thresholds) (Wang et al., 2016; Xie & Yu, 2019) (Figure 4). The transfer effects in the second and third cases could be achieved by adding a more abstract and conceptual representation of the stimulus feature, in which the stimulus inputs could be standardized and thus invariant to stimulus locations, orientations, physical properties, neural encoders, and precisions (Wang et al., 2016).

Our training paradigm and the results have important clinical implications. For patients with central vision loss, such as age-related macular degeneration, the

current effort is to establish a preferred retinal locus (PRL) as the new "fovea" for peripheral viewing (Kwon, Nandy, & Tjan, 2013). This may not be the best idea because long-distance saccades are required to view the targets on the opposite side of the central scotoma. Moreover, PRL-based saccades tend to block the targets with the central scotoma (White & Bedell, 1990; Whittaker, Cummings, & Swieson, 1991) because the old foveating habits cannot be abandoned easily. Our results showed that the same number of trials can produce similar learning effects at multiple orientation and location conditions versus at a single condition (Figure 1). There was also an additional benefit of learning being unspecific. These findings suggest the feasibility of training a preferred retinal annulus (PRA) around the scotoma without much extra efforts. The patients would learn to use the nearest part of the PRA to make shorter and more precise saccades to view a peripheral target, and the eye movements would still be fovea based. Such a PRA training strategy may dramatically speed up the vision training for patients with central scotoma, as supported by our preliminary data in observers with artificial scotoma (Xie, Liu, & Yu, 2018).

Keywords: perceptual learning, orientation, abstraction

Acknowledgments

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