Feature variability determines specificity and transfer in multiorientation feature detection learning

Jun-Ping Zhu

School of Psychological and Cognitive Sciences, and
Beijing Key Laboratory of Behavior and Mental Health,
Peking University, Beijing, China

✉

Jun-Yun Zhang

School of Psychological and Cognitive Sciences, and
Beijing Key Laboratory of Behavior and Mental Health,
Peking University, Beijing, China

✉

Historically, in many perceptual learning experiments, only a single stimulus is practiced, and learning is often specific to the trained feature. Our prior work has demonstrated that multi-stimulus learning (e.g., training-plus-exposure procedure) has the potential to achieve generalization. Here, we investigated two important characteristics of multi-stimulus learning, namely, roving and feature variability, and their impacts on multi-stimulus learning and generalization. We adopted a feature detection task in which an oddly oriented target bar differed by 16° from the background bars. The stimulus onset asynchrony threshold between the target and the mask was measured with a staircase procedure. Observers were trained with four target orientation search stimuli, either with a 5° deviation (30°–35°–40°–45°) or with a 45° deviation (30°–75°–120°–165°), and the four reference stimuli were presented in a roving manner. The transfer of learning to the swapped target–background orientations was evaluated after training. We found that multi-stimulus training with a 5° deviation resulted in significant learning improvement, but learning failed to transfer to the swapped target–background orientations. In contrast, training with a 45° deviation slowed learning but produced a significant generalization to swapped orientations. Furthermore, a modified training-plus-exposure procedure, in which observers were trained with four orientation search stimuli with a 5° deviation and simultaneously passively exposed to orientations with high feature variability (45° deviation), led to significant orientation learning generalization. Learning transfer also occurred when the four orientation search stimuli with a 5° deviation were presented in separate blocks. These results help us to specify the condition under which multistimuli learning produces generalization, which holds potential for real-world applications of perceptual learning, such as vision rehabilitation and expert training.

Introduction

Visual perceptual learning refers to a long-term performance improvement in visual tasks owing to repeated practice (Lu & Dosher, 2022; Sagi, 2011; Watanabe & Sasaki, 2015). Historically, in many perceptual learning experiments, only a single stimulus condition (e.g., a specific orientation) is practiced and learning is often specific to the trained feature and retinal location (Karni & Sagi, 1991). Taking orientation discrimination learning as an example, performance improvement does not transfer to an untrained orthogonal orientation or untrained retinal location (Schoups, Vogels, & Orban, 1995). Such feature and location specificities coincide with orientation selectivity and retinotopic representation of the primary visual cortex (V1) (Hubel & Wiesel, 1959, Hubel & Wiesel, 1962), which has inspired researchers to interpret perceptual learning as a result of training-induced changes specific to the subset of V1 neurons encoding the trained stimulus (Karni & Sagi, 1991; Schoups et al., 1995; Teich & Qian, 2003) or improved readout of early sensory signals specifically activated by the trained stimulus (Dosher & Lu, 1998; Law & Gold, 2008).

However, specificity is a potential problem for practical settings and thus researchers have been heavily invested in exploring methods to overcome this obstacle. Growing research has shown that the degree of learning specificity is influenced by a diversity of factors, such as task difficulty or precision (Ahissar & Hochstein, 1997; Jeter, Dosher, Petrov, & Lu, 2009; Liu, 1999), training amount (Aberg, Tartaglia, & Herzog, 2009; Jeter, Dosher, Liu, & Lu, 2010), stimulus complexity (Bakhtiari, Awada, & Pack, 2020; McGovern, Webb, & Peirce, 2012), state of adaptation

(Harris, Gliksberg, & Sagi, 2012), spatial attention (Donovan & Carrasco, 2018; Donovan, Szpiro, & Carrasco, 2015), training task and psychophysical methods (Green, Kattner, Siegel, Kersten, & Schrater, 2015; Xiong, Xie, & Yu, 2016), and feature reliability (Yashar & Denison, 2017). For example, in a seminal work by Ahissar and Hochstein (1997), training on an odd-element detection task leads to either orientation-specific or orientation-general learning, depending on the difficulty of the training conditions. Training with odd elements that differed from the background elements slightly (e.g., by 16°, a hard task) leads to much more specific learning. In contrast, training with odd elements that differed greatly from the background elements (e.g., by 90°, an easy task) leads to a significant generalization of learning. It should be noted that Ahissar and Hochstein (1997) used the method of constant stimuli to calculate stimulus onset asynchrony (SOA) thresholds with a single-interval (yes/no) procedure. Later, the orientation specificity in feature detection learning was replicated with different threshold measurements, such as, a single interval adaptive (staircase) procedure (Zhang et al., 2010), or with signal detection measures (Yashar & Denison, 2017). The reverse hierarchy theory, which states that learning starts in higher visual areas and only shifts to lower visual areas if the higher visual areas are unable to complete the task, has been proposed to explain the specificity and transfer in perceptual learning (Ahissar & Hochstein, 1997, Ahissar & Hochstein, 2004).

Significant and complete learning transfer across retinal locations or stimuli features have also been demonstrated with novel training paradigms in our serial studies (Hu, Wen, Chen, & Yu, 2021; Wang, Zhang, Klein, Levi, & Yu, 2012; Wang, Zhang, Klein, Levi, & Yu, 2014; Xiao et al., 2008; Xiong, Zhang, & Yu, 2016; Zhang & Yang, 2014; Zhang et al., 2010). Using a double training paradigm and its variation, a training-plus-exposure (TPE) paradigm, in which observers are trained at one location/orientation in tasks known to be location/orientation-specific and either simultaneously or subsequently passively exposed to the transfer location/orientation in an irrelevant task, perceptual learning can completely transfer to the untrained location/orientation. For example, we showed that the TPE procedure could override orientation specificity in a feature-detection learning originally reported by Ahissar and Hochstein (1997). These results challenge the existing specific perceptual learning models by suggesting a more general perceptual learning process. Learning specificity might result from underactivations of untrained visual neurons due to insufficient bottom-up stimulation and/or top-down attention during training (Xiong, Zhang et al., 2016). Furthermore, TPE results demonstrate that the learning transfer between physically distinct orientation or motion stimuli is mutual and complete, suggesting that

perceptual learning can take place at a conceptual level (Wang et al., 2016). Similarly, Kattner, Cochrane, Cox, Gorman, and Green (2017) demonstrate that training on a series of tasks sharing common components can induce the transfer of learning to new tasks with similar components, not as immediate performance improvement, but as an increase in learning rate—a capability that has been dubbed "learning to learn" (Bavelier, Green, Pouget, & Schrater, 2012; Bejjanki et al., 2014; Braun, Mehring, & Wolpert, 2010). These findings support the hypothesis that perceptual learning occurs at a conceptual level where observers learn abstract rules that can be applied to novel features (Wang et al., 2016).

We usually have to face situations with multiple stimuli in daily life, not just with one limited stimulus. A significant factor in multi-stimulus learning is stimulus presentation order. Earlier we demonstrated that when trained with basic stimulus features (e.g., contrast, orientation, motion direction), observers show learning effects when multiple stimuli (e.g., four contrasts: 20%, 30%, 47%, and 63%) are presented in a fixed order, but not in a random order (roving) (Kuai, Zhang, Klein, Levi, & Yu, 2005; Yu, Klein, & Levi, 2004; Zhang et al., 2008). Interestingly, perceptual learning can escape roving disruption when the roving stimuli are sufficiently different (Dosher, Liu, Chu, & Lu, 2020; Tartaglia, Aberg, & Herzog, 2009; Zhang et al., 2008) or tagged with semantic sequence information (Cong & Zhang, 2014). Roving interference is also evident in auditory learning (Amitay, Hawkey, & Moore, 2005; Nahum, Nelken, & Ahissar, 2010). For example, Amitay et al. (2005) reported that a small degree of roving interferes with learning, but a larger degree of roving does not. Nahum et al. (2010) also showed that learning with complex speech stimuli is affected by stimulus variability during training. Such interference can also be avoided when multiple stimuli are presented in a temporal sequence. We propose that, for multi-stimulus learning to occur, the brain needs to conceptually "tag" each stimulus, to switch attention to the appropriate perceptual template (Zhang et al., 2008). However, the previous studies have been based on basic stimulus features, it remains unclear whether roving affects multi-stimulus learning in relatively complex visual tasks, such as the previously mentioned feature detection task.

More significantly, variability can also influence the generalization of multistimulus learning (Raviv, Lupyan, & Green, 2022). Recent training regimes that utilize rich stimulus sets, such as multi-stimulus training (Manenti, Dizaji, & Schwiedrzik, 2023; Xie & Yu, 2020) and off-the-shelf video games encompassing a diverse set of stimulus properties (Deveau, Lovcik, & Seitz, 2014; Deveau & Seitz, 2014), show greater generalization of learning compared with training procedures using a single stimulus. In these studies,

there are two intertwined sources of variability, numerosity (set size, such as when learning from more or fewer distinct examples) and heterogeneity or feature variability (differences between examples). Although numerosity is often taken as a proxy for feature variability, with increased numerosity usually indicating greater feature variability between stimuli (Arnold & Auvray, 2018), these two sources of variability do not necessarily have to align. A few studies have attempted to experimentally tease the two sources of variability apart to explore their relative roles in multi-stimulus learning generalization (Bowman & Zeithamova, 2020; Poletiek & van Schijndel, 2009; Schiff, Ashkenazi, Kahta, & Sasson, 2021). For example, in grammar learning, it has been found that the main predictor of generalization is the diversity of the stimulus set used in the training phase and its statistical coverage of the grammar, but not the mere size of the set (Poletiek & van Schijndel, 2009; Schiff et al., 2021). Similarly, in category learning, high set coherence leads to better generalization, whereas set size has little effect (Bowman & Zeithamova, 2020). However, in the domain of visual perceptual learning, there remains a lack of evidence to clarify the relative contribution of numerosity and feature variability to multi-stimulus learning generalization.

Here we adopted a feature detection task in which target odd elements differed from the background elements by 16° (hard task as in Ahissar & Hochstein, 1997). We also adopted the single interval staircase procedure to measure the SOA threshold as in our previous study (Zhang et al., 2010). In the current study, observers were trained with multiple target orientation search stimuli presented in a roving or block manner. After training, the transfer of learning to the swapped target–background orientations was evaluated. Additionally, we manipulated the feature variability (the deviation between two levels of a feature) by changing the deviation of four orientation search stimuli: either with a 5° deviation (30°–35°–40°–45°) or with a 45° deviation (30°–75°–120°–165°). We aimed to investigate two primary questions. First, we sought to understand whether roving prevents learning from occurring in a relatively complex visual task, a feature detection task. Second, we tried to clarify the relative contribution of numerosity and feature variability to multi-stimulus learning generalization. Our results showed that learning multiple feature stimuli in a roving way did not prevent learning from occurring. Interestingly, multi-stimulus learning with high feature variability (45° deviation) showed much more learning transfer to the swapped orientations than that with low feature variability (5° deviation) (Conditions 1 and 2). For the 5° deviation condition, learning transfer occurred when observers were passively exposed to orientations with high feature variability (Condition 3) or when different reference stimuli were presented

in separate blocks (Condition 4). These results help us to specify the condition under which multi-stimulus learning produces generalization, which is particularly important for real-world applications of perceptual learning, such as vision rehabilitation and expert training.

Methods

Observers and apparatus

A total of 32 observers (undergraduate students in their early 20s) with normal or corrected-to-normal vision participated in this study. All were inexperienced in psychophysical experiments and were unaware of the purposes of the study. This study was approved by the Peking University Institution Review Board. Informed consent was obtained from each observer before testing.

The stimuli were generated with Psychtoolbox-3 software (Pelli, 1997) and presented on a 21-inch Sony G520 color monitor (1024 × 768 pixels; 0.37 × 0.37 mm per pixel; 120 Hz frame rate; 50 cd/m^2 mean luminance). A chin and head rest helped to stabilize the head of an observer. The viewing was binocular at a distance of 2 m. Experiments were run in a dimly lit room. Responses were collected via the computer keyboard.

Stimuli and procedure

The feature detection task mainly consisted of a search stimulus and mask stimulus, which were similar to those used by Ahissar and Hochstein (1997) (Figure 1a). The search stimulus was a bar array. The array consisted of 7 × 7 white bars (22.2 × 1.3 arcmin each) with an interbar distance of 42.5 ± 3.9 arcmin. In one-half of the trials, the search stimulus was composed of target and background orientations. The target was an oddly oriented bar placed at either the second or the sixth bar location of the middle row of the array. The background was other uniformly oriented bars. The target always differed from the background by 16°. In the other one-half of the trials, the search stimulus included only background orientation with all 7 × 7 white bars uniformly oriented. The search stimulus was followed, at various SOAs, by a mask stimulus that was also a 7 × 7 array, with each element containing one pair of white bars oriented at the target and background orientations, and the other pair rotated by 90°.

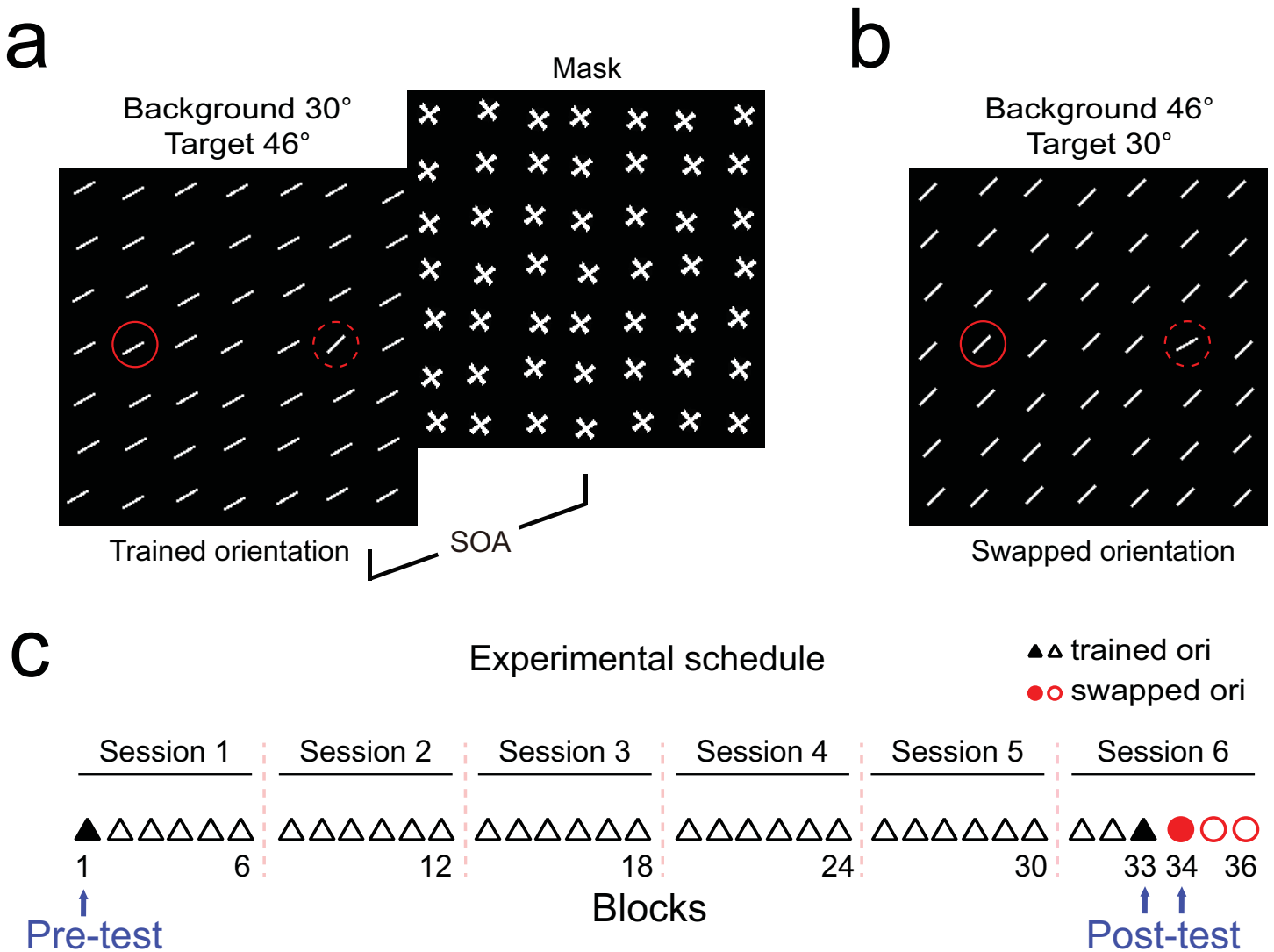The feature detection threshold was measured with a single interval staircase procedure, which was adopted

Figure 1. Stimuli and experimental schedule. (**a**) Stimulus configuration of the feature detection task at trained target–background orientations (46° vs 30°) and mask. The odd element (target) could appear at one of two positions (indicated by red circles that were not present in the actual stimuli). The dashed circle indicates the target. (**b**) Stimulus at untrained target–background swapped orientations (30° vs 46°). The red circle was not present in the actual stimulus. The dashed circle indicates the target. (**c**) Experiments were conducted over six sessions, with one session per day. Each session comprised 6 blocks, resulting in a total of 36 blocks. Observers experienced a pretest with the orientations to be trained (block 1), followed by additional practice blocks until the post-test of the trained orientations (block 33) in session 6. Subsequently, observers were immediately tested with the swapped orientations in block 34 and continued practicing the swapped orientations for two additional blocks (blocks 35–36) to assess further improvements.

from our previous study ([Zhang et al., 2010](#)). Each trial started with a 200-ms fixation display followed by the presentation of the search stimulus for 8.3 ms, which was followed by a 92-ms mask stimulus display (e.g., [Figure 1](#)a). SOA between the search stimulus and the mask stimulus was variable. Following the mask stimulus, the screen went blank until the observer made a response. Observers were asked to report whether the search stimulus array contained an odd element (50% trials) by pressing one of two designated keyboard keys (1 for present and 2 for absent). Observers were

instructed to respond as accurately as possible without speed stress. The intertrial interval was 500 ms. To maintain consistency in data collection, auditory feedback was provided immediately after incorrect responses throughout the entire experiment (including training and test sessions), which was consistent with [Ahissar and Hochstein (1997)](#).

A classical three-down-one-up staircase rule that resulted in a 79.4% convergence level was used to measure the feature detection threshold. The initial SOA values were sufficiently large that the observers

	Orientation deviation	Presentation order	Training paradigm
Condition 1	5° deviation	Roving	Training
Condition 2	45° deviation	Roving	Training
Condition 3	5° deviation	Roving	Training plus exposure
Condition 4	5° deviation	Block	Training

Table 1. Study design. The key differences between the four training conditions exist in the orientation deviation of the four orientation search stimuli, the presentation order of the four orientation search stimuli, and the training paradigm.

could always make a correct discrimination. The step size of the staircase was 0.05 log units. Each staircase consisted of four preliminary reversals and six experimental reversals. A reversal occurs if the stimulus value moves up when it was last moved down, or vice versa. The geometric mean of the six experimental reversals was taken as the threshold for each staircase run.

Experimental design

This study consisted of four training conditions conducted in separate groups of observers. In all four training conditions, with a limited number of exceptions noted below, observers underwent six sessions, with each session consisting of six blocks (Figure 1c). Each session was conducted on a separate day and lasted approximately 1.0 to 1.5 hours. During the training phase, observers repeatedly practiced 4 different orientation search stimuli for 33 blocks, with each block comprising 4 staircases measuring the SOA threshold of the 4 different orientation search stimuli respectively. Subsequently, from block 34 to block 36, observers experienced transfer blocks, in which target–background orientations were swapped, for example, searching a 46° target among a 30° background in previous training blocks became searching a 30° target among a 46° background in transfer blocks (Figure 1b). We considered the estimates from block 1, block 33, and block 34 as the pretest, post-test for the trained orientations, and post-test for the swapped orientations, respectively.

Previous research has demonstrated the existence of orientation search asymmetry, where observers have an advantage in detecting oblique targets among cardinal or near-cardinal distractors over the reverse scenario (Yashar & Denison, 2017). In the current study, we balanced possible orientation search asymmetry between training and transfer among observers. This was achieved by assigning some observers' trained orientations as swapped orientations for other observers, and vice versa.

The key differences between the four training conditions existed in terms of orientation deviation, presentation order, and training paradigm (Table 1). In Condition 1, observers experienced four orientation

search stimuli whose background orientations were 30°, 35°, 40°, and 45°, respectively, with a 5° deviation (Figure 2a). The four orientation search stimuli were run randomly interleaved every trial (roving). Condition 2 was the same as the Condition 1, except that observers experienced four orientation search stimuli whose background orientations were 30°, 75°, 120°, and 165°, respectively, with a 45° deviation (Figure 3a).

Condition 3 was the same as Condition 1, except that during the second to the fifth sessions, each block of feature detection task was followed by a block of exposure task, which was called a TPE procedure (Zhang et al., 2010). In the exposure task, the observers were exposed to the four background orientations with a 45° deviation (30°, 75°, 120°, and 165°) at an SOA fixed at 500 ms, which was near the average pretraining threshold. The exposure task required observers to judge whether the stimuli were bars (uniformly oriented at the background orientations without the odd element presented in 80% of trials) or circles (20% of trials) in each 60-trial block (Figure 4a).

Condition 4 was the same as Condition 1, except that the four orientation search stimuli were presented in separate blocks. Specifically, each block contained four mini-blocks of trials, with each mini-block running an orientation search stimulus separately using a staircase, and the four mini-blocks proceeded in ascending order according to their assigned orientations (30°, 35°, 40°, and 45°).

Statistical analyses

The learning and transfer effects were measured by the percent threshold improvements from pretest to post-test sessions, that is, $100\% \times (\text{Threshold}_{pre} - \text{Threshold}_{post})/\text{Threshold}_{pre}$. Individual improvements were first calculated and then averaged to yield the mean percent improvement (MPI). Threshold improvements were compared against the value 0 with a one-sample t-test. Threshold improvements between training and transfer within a group were compared with a two-tailed paired t test. Threshold improvements across conditions were compared with a one-way ANOVA (analysis of variance).
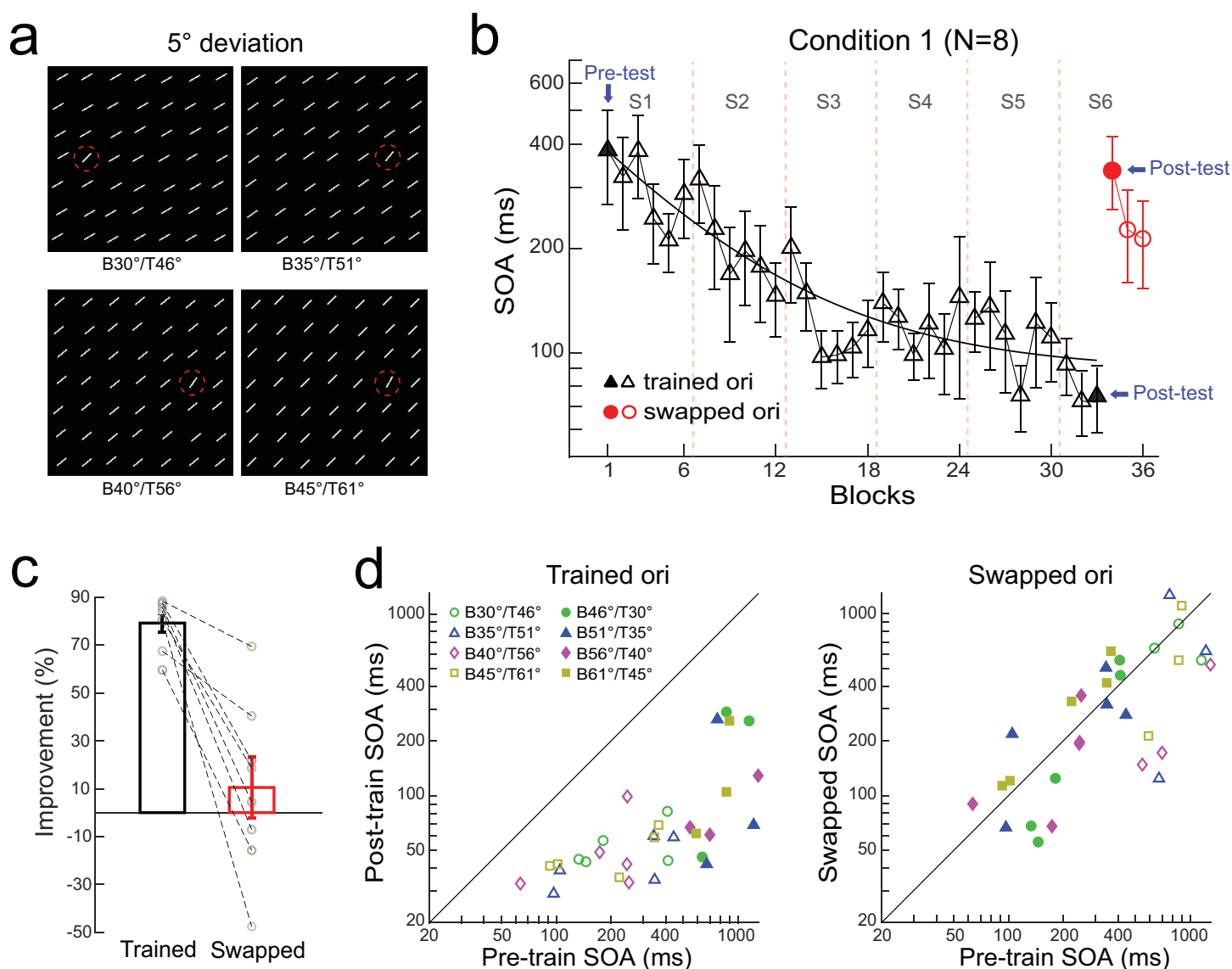
Figure 2. Condition 1: Perceptual learning of four orientation search stimuli with 5° deviation in roving order. (**a**) Stimuli: Four orientation search stimuli whose background orientations are 30°, 35°, 40°, and 45°, respectively, with a 5° deviation. Letters 'B' and 'T' represent background and target orientation, respectively. (**b**) Block-by-block SOA threshold changes at the training (black triangles) and transfer (red circles) orientations. The smooth curve shows exponential function fits. The SOA threshold of each block is averaged from four orientation search stimuli. Sessions 1 through 6 denoted as S1 through S6 are separated visually by light lines, with each session consisting of six blocks. (**c**) Mean percent improvement (bars) and individual percent improvements (circles) at trained and swapped orientations, respectively. The dashed line connected the data from the same observer. (**d**) (Left) Post-training versus pretraining SOA thresholds at four trained orientations. (Right) Post-test SOA thresholds at four swapped target–background orientations versus pretraining SOA thresholds at four trained target–background orientations. Solid and hollow symbols represent different trained or swapped orientations. The y-axes show SOA thresholds on a logarithmic scale. Error bars indicate 1 standard error of the mean. SOA, stimulus onset asynchrony.

Results

Condition 1: Perceptual learning of four orientation search stimuli with a 5° deviation in roving order

To investigate the impact of roving on multi-stimulus learning in a relatively complex visual task and the role of feature variability in learning and transfer, we first had eight observers practice four orientation search stimuli, each deviating by 5° in a roving order (Figure 2a). Considering the complexity of the visual search task, we hypothesized that roving might not impede the occurrence of multi-stimulus learning. Furthermore, we suspected that learning with a 5° deviation between the orientation search stimuli, akin to learning with a single orientation search stimulus in
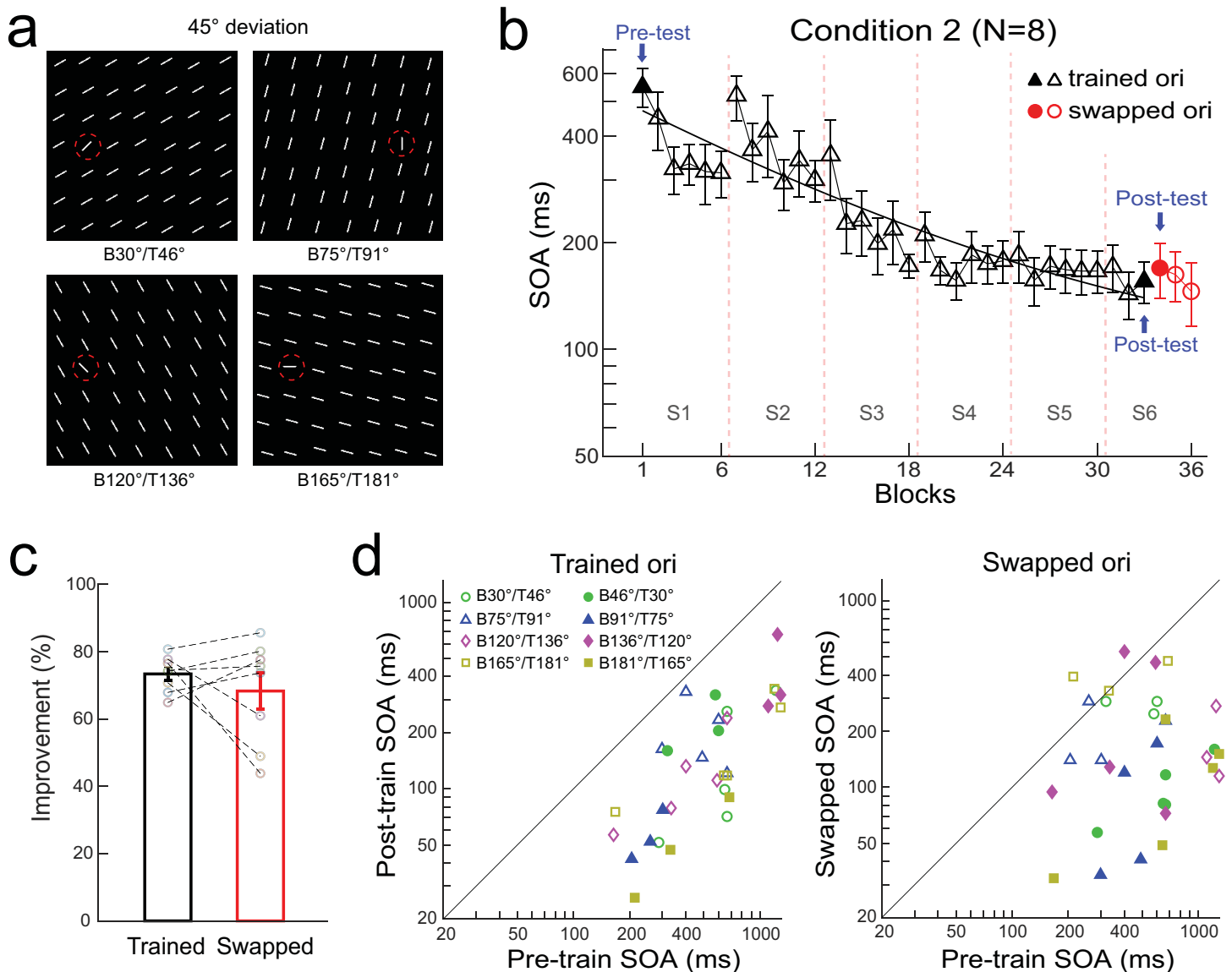
Figure 3. Condition 2. Perceptual learning of four orientation search stimuli with 45° deviation in roving order. (**a**) Stimuli: Four orientation search stimuli whose background orientations are 30°, 75°, 120°, and 165°, respectively, with a 45° deviation. Letters 'B' and 'T' represent background and target orientation, respectively. (**b**) Block-by-block SOA threshold changes at the training (black triangles) and transfer (red circles) orientations. The smooth curve shows exponential function fits. The SOA threshold of each block is averaged from four orientation search stimuli. Sessions 1 through 6 denoted as S1 through S6 are separated visually by light lines, with each session consisting of six blocks. (**c**) Mean percent improvement (bars) and individual percent improvements (circles) at trained and swapped orientations, respectively. The dashed line connected the data from the same observer. (**d**) (Left) Post-training versus pretraining SOA thresholds at four trained orientations. (Right) Post-test SOA thresholds at four swapped target–background orientations versus pretraining SOA thresholds at four trained target–background orientations. Solid and hollow symbols represent different trained or swapped orientations. The y-axes show SOA thresholds on a logarithmic scale. Error bars indicate 1 standard error of the mean. SOA, stimulus onset asynchrony.

the seminal research by Ahissar and Hochstein (1997), would lead to orientation specificity.

Figure 2b shows the changes in block-by-block SOA thresholds, which were averaged from the SOA thresholds of four orientation search stimuli across observers. It is noted that there was no pretest at the swapped target–background orientations as in the study

of Ahissar and Hochstein (1997), so pretest thresholds at the trained target–background orientations were also regarded as pretest thresholds at swapped target–background orientations. The average thresholds of eight observers at the pretest of trained orientations, post-test of trained orientations, and post-test of swapped orientations were 384.2 ± 116.7 ms,
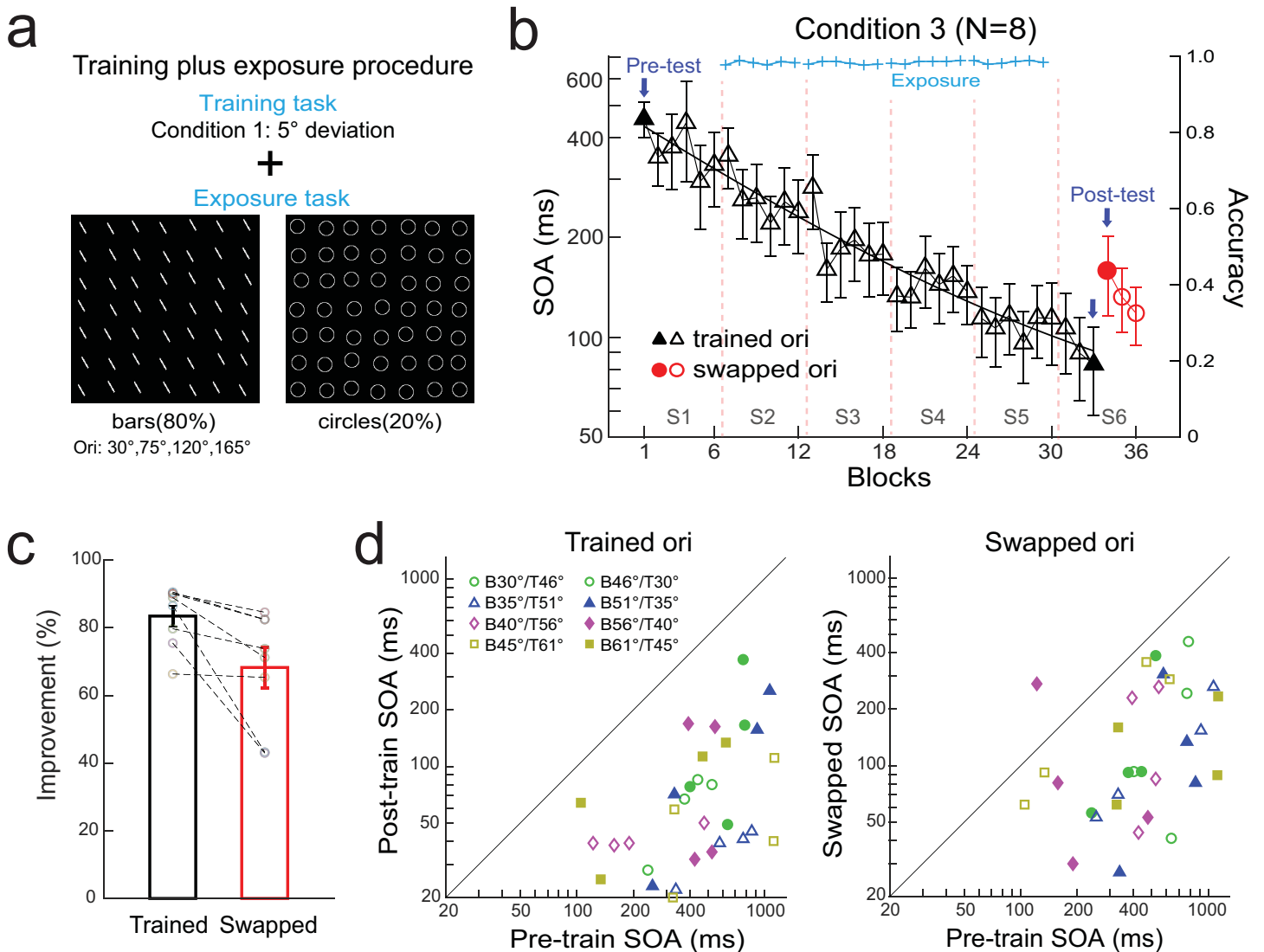
Figure 4. Condition 3. Perceptual learning of four roving orientation search stimuli with 5° deviation under the training-plus-exposure (TPE) procedure. (**a**) Stimuli for exposure task: uniform stimulus array containing background orientations only or containing circles for the bars or circles judgment. Observers are exposed to four background orientations with 45° deviation (e.g., 30°, 75°, 120°, 165°). (**b**) Block-by-block SOA threshold changes at the training (black triangles) and transfer (red circles) orientations. The smooth curve shows exponential function fits. The SOA threshold of each block is averaged from four orientation search stimuli. The accuracy of the exposure task is always near 100% in each block (blue crosses). Session 1 through 6 denoted as S1 through S6 are separated visually by light lines, with each session consisting of six blocks. (**c**) Mean percent improvement (bars) and individual percent improvements (circles) at trained and swapped orientations, respectively. The dashed line connected the data from the same observer. (**d**) (Left) Post-versus pretraining SOA thresholds at four trained orientations. (Right) Post-test SOA thresholds at four swapped target–background orientations versus pretraining SOA thresholds at four trained target–background orientations. Solid and hollow symbols represent different trained or swapped orientations. The y-axes show SOA thresholds on a logarithmic scale. Error bars indicate 1 standard error of the mean. SOA, stimulus onset asynchrony.

76.2 ± 18.5 ms, and 340.1 ± 80.9 ms, respectively ([Figure 2](#)b).

To quantify the learning rate, we used an exponential function $y = y_0 - a\left(1 - e^{-x/\tau}\right)$ to fit the training-induced change of threshold (smooth curve in [Figure 2](#)b), where x was the training block, y_0 was the threshold at $x = 0$, a was the asymptotic threshold with sufficient training, and τ was the time constant corresponding with the training time needed to reach 63% of asymptotic performance ([Levi, Li, Silver, & Chung, 2020](#); [Li, Ngo, Nguyen, & Levi, 2011](#)). The time constant was 8.4 blocks, indicating a relatively fast learning process. [Figure 2](#)d shows the comparisons of the post-training versus pretraining

and the comparisons of swapped versus pretraining SOA thresholds, respectively, for all observers, which were presented in a scatterplot along a unit slope line ($x = y$) and each point reflected one orientation search stimulus for each observer. If data points accumulated under the line, then SOA thresholds were lower at the post-test than at the pretest, indicating obvious learning or transfer.

Figure 2c shows MPI for eight observers and individual percent improvements on trained and swapped orientations respectively. Significant learning for the trained orientations were obtained after training, as the threshold improvements were significantly higher than zero (Figure 2c), $MPI_{trained} = 79.2 \pm 3.6\%$, $t_7 = 21.71$, $p < 0.001$, Cohen's d = 7.68. These results suggested that perceptual learning was evident when four orientation search stimuli with a 5° deviation were practiced in a roving order. However, the percent threshold improvements of swapped orientations were insignificantly different from zero (Figure 2c), $MPI_{swapped} = 10.5 \pm 12.7\%$, $t_7 = 0.83$, $p = 0.43$, Cohen's d = 0.29, and were significantly lower than that of trained orientations (Figure 2c), $t_7 = 5.59$, $p < 0.001$, Cohen's d = 1.98, indicating that learning was mostly orientation specific.

Although learning did not show direct transfer to the swapped orientations from the very first block (block 34), the change rate for the three blocks of swapped orientations (blocks 34–36) in session 6 tended to be faster than the change rate for the first three blocks of trained orientations in session 1 (Figure 2b). Continued training of the swapped orientations produced enormous improvements (Figure 2b), $MPI_{block\ 36/block\ 34} = 30.8 \pm 12.7\%$, $t_7 = 2.43$, $p = 0.046$, Cohen's d = 0.86; in contrast, the initial training of the trained orientations at the first three blocks produced fewer improvements, $MPI_{block\ 3/block\ 1} = 8.9 \pm 12.4\%$, $t_7 = 0.71$, $p = 0.50$, Cohen's d = 0.25. These results indicated increases in the learning rate rather than immediate performance improvement for the swapped orientations, which has been referred to as the learning to learn form of generalization (Bavelier et al., 2012; Kattner et al., 2017).

Condition 2: Perceptual learning of four roving orientation search stimuli with a 45° deviation

Previous studies showed that the escape of roving disruption in multi-stimulus learning depended on variability/similarity between stimuli, with high variability but not low variability free from roving disruption (Dosher et al., 2020; Zhang et al., 2008). We predicted that high feature variability would promote generalization in multi-stimulus learning in the current study. Another eight observers were trained with four orientation search stimuli whose background

orientations were 30°, 75°, 120°, and 165°, respectively, with a 45° deviation (Figure 3a). Figure 3b shows the changes in block-by-block SOA thresholds. The average thresholds of the eight observers at the pretest, post-test of trained orientations, and swapped orientations were 548.9 ± 68.5 ms, 155.5 ± 20.8 ms, and 169.3 ± 29.8 ms, respectively (Figure 3b). An exponential fit $y = y_0 - a$ $(1 - e^{-x/\tau})$ to the data revealed time constants (τ) of 16.6 blocks, indicating a relatively slow learning process compared with Condition 1 whose time constant (τ) was 8.4 blocks.

Significant learning for the trained orientations was obtained after training, as the percent threshold improvements were significantly higher than zero (Figure 3c), $MPI_{trained} = 73.4 \pm 1.9\%$, $t_7 = 39.49$, $p < 0.001$, Cohen's d = 13.96. Besides, an independent sample t-test revealed that threshold improvements in this condition were not significantly different from those in Condition 1, $t_{14} = 1.42$, $p = 0.18$, Cohen's d = 0.71, indicating that feature variability might not affect the learning amount of muti-stimulus learning. The threshold improvements of swapped orientations were also significantly different from zero (Figure 3c), $MPI_{swapped} = 68.3 \pm 5.4\%$, $t_7 = 12.63$, $p < 0.001$, Cohen's d = 4.47, and were insignificantly different from that of trained orientations (Figure 3c), $t_7 = 0.88$, $p = 0.41$, Cohen's d = 0.31, indicating that learning was completely orientation transferable. Continued training of the swapped orientations produced insignificant further improvements (Figure 3b), $MPI_{block\ 36/block\ 34} = 11.0 \pm 10.4\%$, $t_7 = 1.06$, $p = 0.33$, Cohen's d = 0.37, confirming complete improvements of the swapped orientations.

Figure 3d shows the comparisons of the post-versus pretraining and the comparisons of swapped versus pretraining SOA thresholds respectively for all observers. Interestingly, we observed that the detection of an oblique target against cardinal backgrounds (e.g., B91°/T75° or B181°/T165°) was more efficient than the reverse scenario (e.g., B75°/T91° or B165°/T181°), as the orientation search asymmetry reported by Yashar and Denison (2017). Specifically, three observers trained with B91°/T75° or B181°/T165° showed little transfer to the swapped situations B75°/T91° or B165°/T181°, $Threshold_{pre\_B91°/T75°} = 254.7 \pm 27.8$ ms, $Threshold_{post\_B91°/T75°} = 57.0 \pm 10.4$ ms, $Threshold_{swapped\_B75°/T91°} = 189.7 \pm 49.7$ ms; $Threshold_{pre\_B181°/T165°} = 410.0 \pm 142.1$ ms, $Threshold_{post\_B181°/T165°} = 54.3 \pm 18.8$ ms, $Threshold_{swapped\_B165°/T181°} = 400.0 \pm 42.6$ ms. Conversely, five observers trained with B75°/T91° or B165°/T181° showed complete transfer to the swapped situations B91°/T75° or B181°/T165°, $Threshold_{pre\_B75°/T91°} = 491.3 \pm 66.3$ ms, $Threshold_{post\_B75°/T91°} = 199.2 \pm 37.9$ ms, $Threshold_{swapped\_B91°/T75°} = 118.9 \pm 37.4$ ms; $Threshold_{pre\_B165°/T181°} = 793.0 \pm 205.4$ ms,

Threshold$_{post\_B165°/T181°}$ = 185.6 ± 52.0 ms, Threshold$_{swapped\_B181°/T165°}$ = 118.2 ± 36.2 ms. These results confirmed the results reported by Yashar and Denison (2017), showing the transfer depending on the orientation of the target, with full transfer of learning from near-cardinal to oblique targets, but not the reverse.

To exclude the possibility that transfer of learning in 45° deviation (Condition 2) and specificity in 5° deviation (Condition 1) was not due to learning with different deviations, but was due to that swapped orientation in 45° deviation was easier to transfer than that in 5° deviation, we had four observers in 45° deviation perform the untrained 5° deviation condition besides the swapped orientations during the post-test session. Their thresholds in untrained 5° deviation condition (average = 143.9 ± 24.6 ms) were not significantly different from their thresholds of trained orientations (average = 178.8 ± 21.6 ms), because their percent threshold improvements in untrained 5° deviation condition were insignificantly different from that of trained orientations, MPI$_{\_5°\ deviation}$ = 78.4 ± 1.3%, MPI$_{\_trained}$ = 72.7 ± 2.1%, t_3 = 2.18, p = 0.12, Cohen's d = 1.09, indicating that learning for 45° deviation condition could also transfer to a 5° deviation condition. Therefore, it was the learning with different deviations but not the transfer test with different deviations that led to different transfer effects.

Condition 3: The TPE procedure may alleviate the learning specificity of four roving orientation search stimuli with a 5° deviation

Previously, we have demonstrated that using a TPE procedure, in which observers were trained at one orientation and either simultaneously or subsequently passively exposed to the untrained orientation with an irrelevant task, perceptual learning completely transferred to the untrained orientation in tasks known to be orientation specific (Zhang et al., 2010). We expected that passive exposure to high-variability features would facilitate low-variability feature learning transfer to untrained orientations. In Condition 3, we adopted a modified TPE procedure, in which observers were trained with four orientation search stimuli with 5° deviation in a roving order and simultaneously passively exposed to orientations with 45° feature variability, to see whether the orientation specificity in a 5° deviation condition as Condition 1 showed could be eliminated.

Eight new observers were trained with four orientation search stimuli in the 5° deviation condition in a roving way as in Condition 1 (background orientations were 30°, 35°, 40°, and 45°). Besides, they were simultaneously exposed to four background orientations with 45° deviation (e.g., 30°, 75°, 120°, and 165°) in alternative blocks. In the exposure task, the observers were asked to judge whether the stimuli

were bars (uniformly oriented at the background orientations without the odd element presented in 80% of trials) or circles (20% of trials) in each 60-trial block (Figure 4a). The TPE procedure was performed in the same session from the second to the fifth session. Changes in block-by-block SOA thresholds are shown in Figure 4b. The average thresholds of eight observers at the pretest, post-test of trained orientations, and swapped orientations were 454.8 ± 55.6 ms, 83.0 ± 24.6 ms, and 159.0 ± 43.0 ms, respectively (Figure 4b). An exponential fit $y = y_0 - a\,(1 - e^{-x/\tau})$ to the data revealed time constants (τ) of 14.9 blocks, indicating a relatively slow learning process. Figure 4d shows the comparisons of the post-training versus pretraining and the comparisons of swapped versus pretraining SOA thresholds, respectively, for all observers.

Significant learning for the trained orientations was obtained after training, as the threshold improvements were significantly greater than zero (Figure 4c), MPI$_{\_trained}$ = 83.4 ± 3.1%; t_7 = 26.70, p < 0.001, Cohen's d = 9.44. Meanwhile, the accuracy of the exposure task was always near 100%, indicating that observers performed well in the exposure task. The threshold improvements of swapped orientations were also significantly different from zero (Figure 4c), MPI$_{\_swapped}$ = 68.3 ± 5.9%, t_7 = 11.48, p < 0.001, Cohen's d = 4.06, but were significantly lower than those of trained orientations (Figure 4c), t_7 = 2.86, p = 0.024, Cohen's d = 1.01, indicating that the learning effect showed incomplete transfer to the swapped orientations with the modified TPE procedure. Continued training of the swapped orientations produced insignificant further improvements (Figure 4b), MPI$_{\_block\ 36/block\ 34}$ = 12.4 ± 8.9%, t_7 = 1.40, p = 0.21, Cohen's d = 0.49, suggesting substantial learning transfer to the swapped orientations has occurred after the TPE training.

Condition 4: Perceptual learning of four orientation search stimuli with a 5° deviation in a blocked condition

Previous studies have shown that learning occurred when multiple stimuli were presented in a fixed order, but not in a random order (roving) (Kuai et al., 2005; Yu, Klein, & Levi, 2004; Zhang et al., 2008). In addition, it has been shown that training schedules, such as when learning from the same examples, but under more or less varied practice schedules, had an impact on learning and transfer (Raviv et al., 2022). Training with four roving orientations with a 5° deviation in Condition 1 might contain cross-trial uncertainty. Such uncertainty might be available and even become stronger at the swapped target–background orientations, leading to orientation specificity. We speculated that the presentation of fixed order might reduce the cross-trial uncertainty and increase the feature variability. Therefore, training
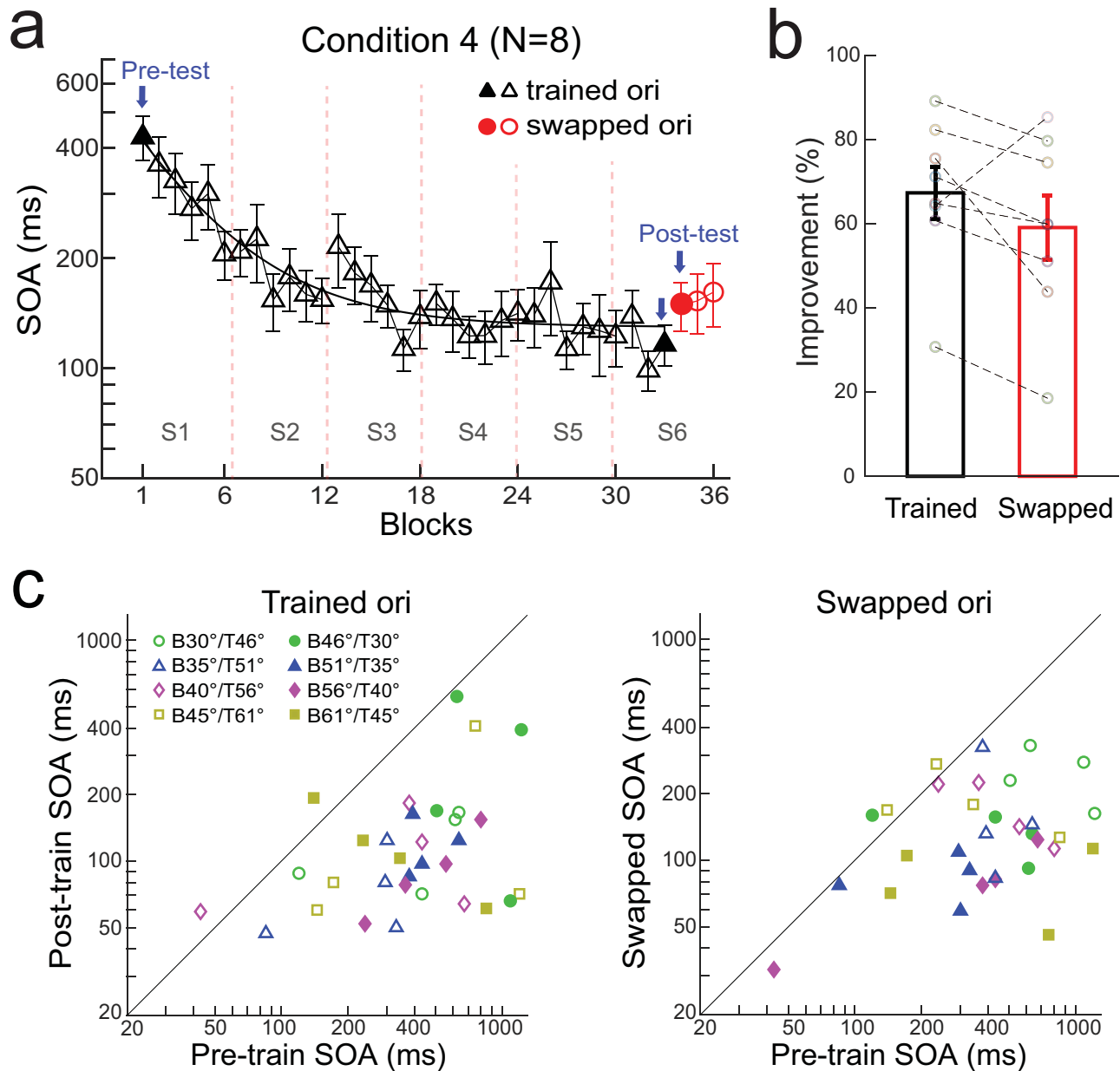
Figure 5. Condition 4. Perceptual learning of four orientation search stimuli with 5°deviation in a blocked design. (**a**) Block-by-block SOA threshold changes at the training (black triangles) and transfer (red circles) orientations. The smooth curve shows exponential function fits. The SOA threshold of each block is averaged from four orientation search stimuli. Sessions 1 through 6 denoted as S1 through S6 are separated visually by light lines, with each session consisting of six blocks. (**b**) Mean percent improvement (bars) and individual percent improvements (circles) at trained and swapped orientations, respectively. The dashed line connected the data from the same observer. (**c**) (Left) Post-training versus pretraining SOA thresholds at four trained orientations. (Right) Post-test SOA thresholds at four swapped target–background orientations versus pretraining SOA thresholds at four trained target–background orientations. Solid and hollow symbols represent different trained or swapped orientations. The *y* axes show SOA thresholds on a logarithmic scale. Error bars indicate 1 standard error of the mean. SOA, stimulus onset asynchrony.

with four orientations in a fixed order would facilitate the learning transfer to swapped target–background orientations.

We had eight new observers practice four orientation search stimuli with a 5° deviation in a blocked

condition. Each experimental block contained four min-blocks of trials (or four staircases) for four background orientations (30°, 35°, 40°, and 45°) measured in ascending order. The block-by-block SOA threshold changes were shown in Figure 5a. The average
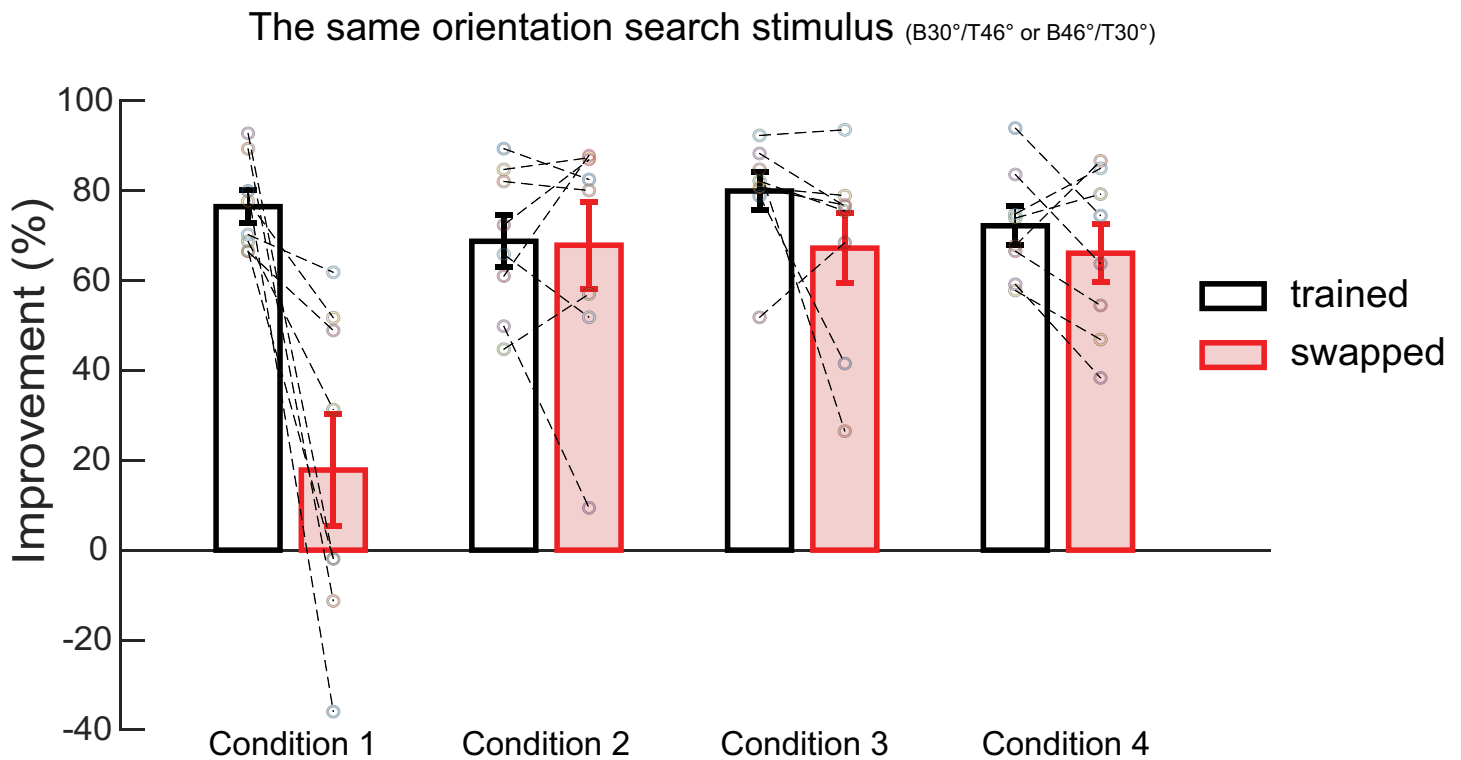
Figure 6. Learning and transfer of a common orientation search stimulus across four conditions. Mean percent improvement (bars) and individual percent improvements (circles) at trained and swapped orientations, respectively.

thresholds of eight observers at the pretest, post-test of trained orientations and swapped orientations were 428.0 ± 59.1 ms, 116.0 ± 14.7 ms, and 148.5 ± 22.6 ms, respectively. An exponential fit $y = y_0 - a \, (1 - e^{-x/\tau})$ to the data revealed time constants (τ) of 5.1 blocks, indicating a fast learning process (Figure 5a). Figure 5c shows the comparisons of the post-training versus pretraining and the comparisons of swapped versus pretraining SOA thresholds, respectively, for all observers.

Significant learning for trained orientations was obtained after training, as the percent threshold improvements were significantly higher than zero (Figure 5b), $\text{MPI}_{\text{trained}} = 67.3 \pm 6.2\%$; $t_7 = 10.79$, $p < 0.001$, Cohen's d = 3.82. The threshold improvements of swapped orientations were also significantly different from zero (Figure 5b), $\text{MPI}_{\text{swapped}} = 59.1 \pm 7.7\%$, $t_7 = 7.71$, $p < 0.001$, Cohen's d = 2.73, and were insignificantly different from that of trained orientations (Figure 5b), $t_7 = 1.62$, $p = 0.15$, Cohen's d = 0.57, indicating that the learning effects transfer to the swapped orientations. Continued training of the swapped orientations did not produce further improvements (Figure 5a), $\text{MPI}_{\text{block 36/block 34}} = -7.3 \pm 15.3\%$, $t_7 = -0.48$, $p = 0.65$, Cohen's d = –0.17, confirming that complete learning transfer to the swapped orientations has occurred after training.

Summary: Comparing the same orientation search stimulus across four conditions

For better cross-condition comparison of learning and transfer, we separately analyzed the same orientation search stimulus (B30°/T46° or B46°/T30°) across four conditions. This orientation search stimulus does not include cardinal orientation, which could avoid the impact of orientation search asymmetry on learning transfer. Although percent threshold improvements at the trained orientation in Condition 2 seemed slightly lower, a one-way ANOVA indicated that improvements across the four conditions did not differ significantly (Figure 6), $\text{MPI}_{\text{trainned}} = 76.4 \pm 3.6\%$, $68.7 \pm 5.8\%$, $79.9 \pm 4.3\%$, and $72.2 \pm 4.3\%$, respectively; $F_{(3, 28)} = 1.14$, $p = 0.35$, $\eta^2 = 0.11$, suggesting that training conditions such as feature variability might not impact the amount of learning. In contrast, the improvements for the swapped orientation at post-test varied significantly across four conditions, $\text{MPI}_{\text{swapped}} = 17.8 \pm 12.5\%$, $67.8 \pm 9.7\%$, $67.2 \pm 7.8\%$, and $66.1 \pm 6.4\%$, respectively; $F_{(3, 28)} = 6.88$, $p = 0.001$, $\eta^2 = 0.42$. Post hoc tests using the LSD correction revealed that improvements in Condition 1 were significantly inferior to those of the other three conditions ($ps < 0.01$), whereas the improvements for the other three conditions were equivalent ($ps > 0.9$),

confirming that learning multiple roving stimuli with low variability led to learning specificity to trained orientations.

Discussion

In the current study, we observed that roving did not prevent the acquisition of multiorientation feature detection learning. More important, the feature variability of these stimuli played a crucial role in the generalization of learning when presented in a roving order. Specifically, roving stimuli with high feature variability (45° deviation) exhibited significant transfer effects to the swapped orientations, unlike those with low feature variability (5° deviation). Additionally, passive exposure to orientations with high variability using a modified TPE procedure or presenting the four target orientation search stimuli in separate blocks facilitated the transfer of learning with low feature variability to the swapped orientations. These findings help to specify the conditions under which multi-stimulus learning leads to generalization, potentially inspiring the development of efficient training paradigms in clinical settings.

We demonstrated that multi-stimulus learning in a relatively complex feature detection task is evident even when different stimuli are presented in a roving manner. These results are unlike the evidence in simple discrimination tasks involving low-level visual features like contrast and orientation, in which perceptual learning occurs only when multiple stimuli are presented in a fixed order (e.g., blocked condition), but not in a roving order (Adini, Wilkonsky, Haspel, Tsodyks, & Sagi, 2004; Yu et al., 2004; Nahum et al., 2010). Yotsumoto, Chang, Watanabe, and Sasaki (2009) reported significant learning improvement in a texture discrimination task (TDT), similar to the feature detection task used in this study, which requires the temporal separation of the very brief target and the mask, regardless of whether the stimulus properties are fixed or a random mix of different backgrounds and target orientations. Subsequently, Wang, Cong, and Yu (2013) showed that temporal learning accounts for most of the overall TDT improvement, indicating that TDT learning is mostly temporal learning. Both TDT and feature detection learning may speed up the temporal processing or narrow the temporal window of attention (temporal resolution) to distinguish the target from the mask at shorter SOAs (Polat, Ma-Naim, & Spierer, 2009; Sterkin, Yehezkel, Bonneh, Norcia, & Polat, 2009). Based on this finding, we speculate that the brain could still tag different features in feature detection tasks and switch attention to the appropriate perceptual template, even when different features are presented in a roving manner so that roving does

not prevent learning from occurring (Zhang et al., 2008).

Here we found that roving with low feature variability (5° deviation) resulted in learning specificity, while increased feature variability (45° deviation) in multi-stimulus learning led to a generalization of learning. Learning under both conditions involves the same number of stimuli, indicating that numerosity alone is not particularly beneficial; instead, heterogeneity and feature variability drive the variability effect. Although numerosity is frequently taken as a proxy for heterogeneity, our results are in line with the evidence from grammar learning and category learning, indicating that the two sources of variety (numerosity and heterogeneity) do not always have to coincide and it is often not the number of items or experiences per se that drive variability benefits (Bowman & Zeithamova, 2020; Poletiek & van Schijndel, 2009; Schiff et al., 2021). Meanwhile, we found that learning in the 45° deviation condition took more time to reach 63% of the asymptotic performance compared with the 5° deviation condition, although the learning improvement in both conditions was equivalent. These results are, thus, consistent with some discussion by Raviv et al. (2022) that "Learning from less variable input is often fast, but may fail to generalize to new stimuli; learning with more variable input is initially slower, but typically yields better generalization," which has been shown in other research fields, such as motor learning and language acquisition (Clopper & Pisani, 2004; Huet et al., 2011).

Our previous TPE studies have shown that perceptual learning can achieve transfer if the observers receive additional exposure to the transfer orientation or location via an irrelevant task (Xiao et al., 2008; Xiong, Zhang et al., 2016; Zhang et al., 2010). Here, we further demonstrated that a modified TPE procedure, in which observers were trained with multiple stimulus feature detection with a 5° deviation and simultaneously passively exposed to orientations with a high feature variability, equivalent to adding task-irrelevant variability, enabled learning transfer. This finding expands our understanding of learning transfer, suggesting that the exposure should not be restricted to the transfer orientation. It also supports our understanding of perceptual learning at a conceptual level, which might share a common mechanism with category learning (Hu et al., 2021; Wang et al., 2016; Xie & Yu, 2020; Xiong et al., 2022). Xie and Yu (2020) propose that some high-level processes may abstract stimulus evidence from multiple stimulus conditions, and such learning might engage higher-level orientation-invariant representation. It is most likely that exposure to greater variability facilitates the formation of more abstract knowledge and leads to an improved ability to generalize learning to new contexts. Recently, Manenti et al. (2023) trained a

deep neural network model designed by Wenliang and Seitz (2018) under high and low task-irrelevant variability conditions, indicating that the networks develop invariant representations of the task-irrelevant feature when trained with highly varied inputs. These invariant neurons are more prevalent in the higher-order visual cortex, where neurons also have larger receptive fields. So far, the locus of perceptual learning is still inconclusive. Vogels (2023) indicated that the different results between earlier investigations (Schoups, Vogels, Qian, & Orban, 2001; Yang & Maunsell, 2004) on the role of region V1 in learning fine orientation discrimination may be influenced by the stimulus variability in perceptual learning. This point resonates with the viewpoint of Maniglia and Seitz (2018), suggesting that "the distribution of learning across the neural system depends upon the details of the training procedure and the characteristics of the individual being trained."

How perceptual training parameters impact the generalizability of learning is of sustained importance to the field of visual perception (Lu & Dosher, 2022). Here we show one kind of training parameter, feature variability, impacts learning generalization in multi-stimulus learning. Why does high feature variability lead to generalization? Training with a single stimulus or low-variability stimuli may recruit a limited neural population (Fahle, 2004) and unwittingly promote the overfitting of specific stimuli (Sagi, 2011). One related explanation is that specificity is a consequence of sensory adaptation owing to repeated stimulation. Harris et al. (2012) reported that generalization occurs when task-irrelevant dummy trials are inserted between the main task, which is equivalent to adding task-irrelevant variability. They propose that counteracting adaptation arising during prolonged training is beneficial for generalization. Changing the orientation from 5° (Condition 1) to 45° deviation (Condition 2) or adding task-irrelevant variability (Condition 3) probably alters intertrial adaptation effects, with less sensory adaptation in Conditions 2 and 3. Therefore, reduced adaptation in these two conditions during training most likely results in learning generalization. Another explanation from category learning suggests that exposure to too few instances increases the likelihood that the experienced items are not representative of the category and are insufficient for determining which characteristics predict category membership (Raviv et al., 2022). In contrast, exposure to stimuli with high variability helps the brain to approximate the real distribution in the world, leading to a higher probability of generalizing outside the examples' range (Tenebaum & Griffiths, 2001; Xu & Tenenbaum, 2007).

We found that transfer occurred in a 5° deviation condition when stimuli were presented in a fixed order rather than in roving order, although roving did not prevent learning from occurring. These results align with prior research indicating that training schedules, such as the order in which examples are presented or the interval between them, influence learning and transfer when learning from the same instances (Raviv et al., 2022). For example, compared with massed training (e.g., when learning events occur in succession), spaced training (e.g., when learning events are distributed over time) often leads to better learning and broader transfer of motor skills (Keller, Li, Weiss, & Relyea, 2006; Travlos, 2010) and novel categories (Cepeda, Vul, Rohrer, Wixted, & Pashler, 2008; Vlach & Sandhofer, 2012; Vlach, Sandhofer, & Kornell, 2008). It is hypothesized that varying practice regimens can highlight potential differences between similar variations of the same basic action or category, which in turn results in a more thorough representation and the elaboration of task-relevant information (Raviv et al., 2022). Additionally, spaced training might improve retrieval abilities through a cycle of forgetting and reconstructing or increase the amount and/or richness of memory traces and association cues that may be used for retrieval and recall later on (Howard & Kahana, 2002; Vlach et al., 2008).

Several limitations in this study warrant discussion. First, we measured the SOA thresholds using a single-interval (yes/no) task as Ahissar and Hochstein (1997), but with a staircase procedure instead of the method of constant stimuli. Xiong, Xie et al. (2016) demonstrated the importance of using appropriate psychophysical methods in training to reduce location specificity in perceptual learning. Further evidence is needed to determine whether the current results are specific to the particular psychophysical method. Second, it is claimed that by using trial-by-trial feedback in a single interval procedure, the observers were induced to adopt a neutral response criterion (Kaernbach, 1990). However, it is unclear whether swapping the target and background orientations between training and transfer influences the decision criteria. Yashar and Denison (2017) evaluated the changes in perceptual sensitivity (d') and response bias (c) for each SOA in feature detection learning, showing that lower sensitivity and more conservative bias with shorter SOAs. Future studies from different approaches (e.g., a signal detection approach) could offer the estimation of response bias changes. Third, we used swapped orientation in the transfer test, which mirrored the seminal work of Ahissar and Hochstein (1997). However, given that the same orientations appear in both training and transfer, we do not know at this point whether this finding represents a classic learning transfer to an untrained stimulus or embodies a different concept, such as learning the background orientation. Further exploration combining neurological techniques is necessary for understanding the mechanisms of this learning. Last, our study only tested three blocks of swapped orientations during the post-test, which is insufficient to examine the complete form of learning

to learn (Bavelier et al., 2012; Kattner et al., 2017). Recently, Cochrane and Green (2021) differentiated two ways of generalization—direct transfer and learning to learn—by examining the functional form of learning generalization, in a time-dependent fashion, in conjunction with an investigation of the functions characterizing initial learning. Future investigations on learning and generalization should carefully study the functional form of perceptual learning on the by-person and by-trial levels, where the mechanisms of learning are expected to act.

Our study could help to optimize training procedures in real-world applications of perceptual learning. A growing body of research has demonstrated the benefits of perceptual training for people with visual deficits, such as amblyopia (Levi & Polat, 1996; Liu & Zhang, 2018, 2019; Zhang et al., 2014), macular degeneration (Chung, 2011; Maniglia et al., 2016), cortical blindness (Das, Tadin, & Huxlin, 2014; Herpich et al., 2019), presbyopia (Polat et al., 2012), and dyslexia (Gori, Seitz, Ronconi, Franceschini, & Facoetti, 2016). In addition, numerous approaches aim to exploit perceptual learning in the development of expert training, such as athletes (Appelbaum & Erickson, 2018; Deveau, Ozer, & Seitz, 2014), and medical experts (Kellman, 2013). However, specificity could be a major obstacle to an effective training procedure (Bavelier et al., 2010; Levi & Li, 2009). Fortunately, studies have shown that the multi-stimulus training approach to perceptual learning can increase generalization (Deveau, Lovcik et al., 2014; Deveau & Seitz, 2014; Fulvio, Green, & Schrater, 2014), ameliorate the effects of presbyopia and provide a promise to improve visual function for individuals suffering from low vision (Deveau & Seitz, 2014). In terms of the application of perceptual learning (Lu, Lin, & Dosher, 2016), for better generalization, future training procedures should be taken into account using multiple stimuli with high or clear feature variability to counteract overtraining.

Keywords: perceptual learning, feature variability, roving, specificity, transfer

Acknowledgments

Corresponding author: Jun-Yun Zhang.
Email: zhangjunyun@pku.edu.cn.
Address: School of Psychological and Cognitive Sciences, and Beijing Key Laboratory of Behavior and Mental Health, Peking University, Beijing 100871, China.

References

Aberg, K. C., Tartaglia, E. M., & Herzog, M. H. (2009). Perceptual learning with Chevrons requires a minimal number of trials, transfers to untrained directions, but does not require sleep. *Vision Research, 49*(16), 2087–2094, https://doi.org/10.1016/j.visres.2009.05.020.

Adini, Y., Wilkonsky, A., Haspel, R., Tsodyks, M., & Sagi, D. (2004). Perceptual learning in contrast discrimination: The effect of contrast uncertainty. *Journal of Vision, 4*(12), 993–1005, https://doi.org/10.1167/4.12.2.

Ahissar, M., & Hochstein, S. (1997). Task difficulty and the specificity of perceptual learning. *Nature, 387*(6631), 401–406, https://doi.org/10.1038/387401a0.

Ahissar, M., & Hochstein, S. (2004). The reverse hierarchy theory of visual perceptual learning. *Trends in Cognitive Science, 8*(10), 457–464, http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=15450510.

Amitay, S., Hawkey, D. J., & Moore, D. R. (2005). Auditory frequency discrimination learning is affected by stimulus variability [Research Support, Non-U.S. Gov't]. *Percept Psychophys, 67*(4), 691–698, http://www.ncbi.nlm.nih.gov/pubmed/16134462.

Appelbaum, L. G., & Erickson, G. (2018). Sports vision training: A review of the state-of-the-art in digital training techniques. *International Review of Sport and Exercise Psychology, 11*(1), 160–189, https://doi.org/10.1080/1750984x.2016.1266376.

Arnold, G., & Auvray, M. (2018). Tactile recognition of visual stimuli: Specificity versus generalization of perceptual learning [Article]. *Vision Research, 152*, 40–50, https://doi.org/10.1016/j.visres.2017.11.007.

Bakhtiari, S., Awada, A., & Pack, C. C. (2020). Influence of stimulus complexity on the specificity of visual perceptual learning. *Journal of Vision, 20*(6), Article 13, https://doi.org/10.1167/jov.20.6.13.

Bavelier, D., Green, C. S., Pouget, A., & Schrater, P. (2012). Brain plasticity through the life span: Learning to learn and action video games. *Annual Review of Neuroscience, 35*, 391–416, https://doi.org/10.1146/annurev-neuro-060909-152832.

Bavelier, D., Levi, D. M., Li, R. W., Dan, Y., & Hensch, T. K. (2010). Removing brakes on adult brain plasticity: from molecular to behavioral interventions. *Journal of Neuroscience, 30*(45), 14964–14971, https://doi.org/10.1523/JNEUROSCI.4812-10.2010.

Bejjanki, V. R., Zhang, R. Y., Li, R. J., Pouget, A., Green, C. S., Lu, Z. L., . . . Bavelier, D. (2014). Action video game play facilitates the development of better perceptual templates. *Proceedings of the National Academy of Sciences of the United States of America, 111*(47), 16961–16966, https://doi.org/10.1073/pnas.1417056111.

Bowman, C. R., & Zeithamova, D. (2020). Training set coherence and set size effects on concept generalization and recognition [Article]. *Journal of Experimental Psychology—Learning Memory and Cognition, 46*(8), 1442–1464, https://doi.org/10.1037/xlm0000824.

Braun, D. A., Mehring, C., & Wolpert, D. M. (2010). Structure learning in action. *Behavioural Brain Research, 206*(2), 157–165, https://doi.org/10.1016/j.bbr.2009.08.031.

Cepeda, N. J., Vul, E., Rohrer, D., Wixted, J. T., & Pashler, H. (2008). Spacing effects in learning: A temporal ridgeline of optimal retention. *Psychological Science, 19*(11), 1095–1102, https://doi.org/10.1111/j.1467-9280.2008.02209.x.

Chung, S. T. L. (2011). Improving reading speed for people with central vision loss through perceptual learning. *Investigative Ophthalmology & Visual Science, 52*(2), 1164–1170, https://doi.org/10.1167/iovs.10-6034.

Clopper, C. G., & Pisani, D. B. (2004). Effects of talker variability on perceptual learning of dialects. *Language and Speech, 47*, 207–239, https://doi.org/10.1177/00238309040470030101.

Cochrane, A., & Green, C. S. (2021). Assessing the functions underlying learning using by-trial and by-participant models: Evidence from two visual perceptual learning paradigms. *Journal of Vision, 21*(13), 1–16, https://doi.org/10.1167/jov.21.13.5.

Cong, L. J., & Zhang, J. Y. (2014). Perceptual learning of contrast discrimination under roving: The role of semantic sequence in stimulus tagging. *Journal of Vision, 14*(13), https://doi.org/10.1167/14.13.1.

Das, A., Tadin, D., & Huxlin, K. R. (2014). Beyond blindsight: Properties of visual relearning in cortically blind fields. *The Journal of Neuroscience, 34*(35), 11652–11664, https://doi.org/10.1523/jneurosci.1076-14.2014.

Deveau, J., Lovcik, G., & Seitz, A. R. (2014). Broad-based visual benefits from training with an integrated perceptual-learning video game. *Vision Research, 99*, 134–140, https://doi.org/10.1016/j.visres.2013.12.015.

Deveau, J., Ozer, D. J., & Seitz, A. R. (2014). Improved vision and on-field performance in baseball through perceptual learning. *Current Biology, 24*(4), R146–R147, https://doi.org/10.1016/j.cub.2014.01.004.

Deveau, J., & Seitz, A. R. (2014). Applying perceptual learning to achieve practical changes in vision. *Frontiers in Psychology, 5*, 1166, https://doi.org/10.3389/fpsyg.2014.01166.

Donovan, I., & Carrasco, M. (2018). Endogenous spatial attention during perceptual learning facilitates location transfer. *Journal of Vision, 18*(11), 7, https://doi.org/10.1167/18.11.7.

Donovan, I., Szpiro, S., & Carrasco, M. (2015). Exogenous attention facilitates location transfer of perceptual learning. *Journal of Vision, 15*(10), 11, https://doi.org/10.1167/15.10.11.

Dosher, B. A., Liu, J., Chu, W., & Lu, Z.-L. (2020). Roving: The causes of interference and re-enabled learning in multi-task visual training. *Journal of Vision, 20*(6), 9, https://doi.org/10.1167/jov.20.6.9.

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 of the United States of America, 95*(23), 13988–13993, https://doi.org/10.1073/pnas.95.23.13988.

Fahle, M. (2004). Perceptual learning: A case for early selection. *Journal of Vision, 4*(10), 879–890, https://doi.org/10.1167/4.10.4.

Fulvio, J. M., Green, C. S., & Schrater, P. R. (2014). Task-specific response strategy selection on the basis of recent training experience. *PLoS Computational Biology, 10*(1), e1003425, https://doi.org/10.1371/journal.pcbi.1003425.

Gori, S., Seitz, A. R., Ronconi, L., Franceschini, S., & Facoetti, A. (2016). Multiple causal links between magnocellular-dorsal pathway deficit and developmental dyslexia. *Cerebral Cortex, 26*(11), 4356–4369, https://doi.org/10.1093/cercor/bhv206.

Green, C. S., Kattner, F., Siegel, M. H., Kersten, D., & Schrater, P. R. (2015). Differences in perceptual learning transfer as a function of training task. *Journal of Vision, 15*(10), 5, https://doi.org/10.1167/15.10.5.

Harris, H., Gliksberg, M., & Sagi, D. (2012). Generalized perceptual learning in the absence of sensory adaptation. *Current Biology, 22*(19), 1813–1817, https://doi.org/10.1016/j.cub.2012.07.059.

Herpich, F., Melnick, M. D., Agosta, S., Huxlin, K. R., Tadin, D., & Battelli, L. (2019). Boosting learning efficacy with noninvasive brain stimulation in intact and brain-damaged humans. *Journal of Neuroscience Research, 39*(28), 5551–5561, https://doi.org/10.1523/JNEUROSCI.3248-18.2019.

Howard, M. W., & Kahana, M. J. (2002). A distributed representation of temporal context. *Journal of Mathematical Psychology, 46*(3), 269–299, https://doi.org/10.1006/jmps.2001.1388.

Hu, D.-Z., Wen, K., Chen, L.-H., & Yu, C. (2021). Perceptual learning evidence for supramodal representation of stimulus orientation at a conceptual level. *Vision Research, 187*, 120–128, https://doi.org/10.1016/j.visres.2021.06.010.

Hubel, D. H., & Wiesel, T. N. (1959). Receptive fields of single neurones in the cat's striate cortex. *Journal of Physiology, 148*(3), 574–591, https://doi.org/10.1113/jphysiol.1959.sp006308.

Hubel, D. H., & Wiesel, T. N. (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *Journal of Physiology, 160*(1), 106–154, https://doi.org/10.1113/jphysiol.1962.sp006837.

Huet, M., Jacobs, D. M., Camachon, C., Missenard, O., Gray, R., & Montagne, G. (2011). The education of attention as explanation of variability of practice effects: Learning the final approach phase in a flight simulator. *Journal of Experimental Psychology—Human Perception and Performance, 37*(6), 1841–1854, https://doi.org/10.1037/a0024386.

Jeter, P. E., Dosher, B. A., Liu, S. H., & Lu, Z. L. (2010). Specificity of perceptual learning increases with increased training. *Vision Research, 50*(19), 1928–1940, https://doi.org/10.1016/j.visres.2010.06.016.

Jeter, P. E., Dosher, B. A., Petrov, A., & Lu, Z. L. (2009). Task precision at transfer determines specificity of perceptual learning. *Journal of Vision, 9*(3), 1, 1–13, https://doi.org/Artn110.1167/9.3.1.

Kaernbach, C. (1990). A Single-Interval Adjustment-matrix (Siam) procedure for unbiased adaptive testing. *Journal of the Acoustical Society of America, 88*(6), 2645–2655, https://doi.org/10.1121/1.399985.

Karni, A., & Sagi, D. (1991). Where practice makes perfect in texture discrimination: Evidence for primary visual cortex plasticity. *Proceedings of the National Academy of Sciences of the United States of America, 88*(11), 4966–4970, https://doi.org/10.1073/pnas.88.11.4966.

Kattner, F., Cochrane, A., Cox, C. R., Gorman, T. E., & Green, C. S. (2017). Perceptual learning generalization from sequential perceptual training as a change in learning rate. *Current Biology, 27*(6), 840–846, https://doi.org/10.1016/j.cub.2017.01.046.

Keller, G. J., Li, Y., Weiss, L. W., & Relyea, G. E. (2006). Contextual interference effect on acquisition and retention of pistol-shooting skills. *Perceptual and Motor Skills, 103*(1), 241–252, https://doi.org/10.2466/pms.103.1.241-252.

Kellman, P. J. (2013). Adaptive and perceptual learning technologies in medical education and training. *Military Medicine, 178*(10), 98–106, https://doi.org/10.7205/Milmed-D-13-00218.

Kuai, S. G., Zhang, J. Y., Klein, S. A., Levi, D. M., & Yu, C. (2005). The essential role of stimulus temporal patterning in enabling perceptual learning. *Nature Neuroscience, 8*(11), 1497–1499, https://doi.org/10.1038/nn1546.

Law, C.-T., & Gold, J. I. (2008). Neural correlates of perceptual learning in a sensory-motor, but not a sensory, cortical area. *Nature Neuroscience, 11*(4), 505–513, https://doi.org/10.1038/nn2070.

Levi, D. M., & Li, R. W. (2009). Perceptual learning as a potential treatment for amblyopia: A mini-review. *Vision Research, 49*(21), 2535–2549, https://doi.org/10.1016/j.visres.2009.02.010.

Levi, D. M., Li, R. W., Silver, M. A., & Chung, S. T. L. (2020). Sequential perceptual learning of letter identification and "uncrowding" in normal peripheral vision: Effects of task, training order, and cholinergic enhancement. *Journal of Vision, 20*(4), https://doi.org/10.1167/jov.20.4.24.

Levi, D. M., & Polat, U. (1996). Neural plasticity in adults with amblyopia. *Proceedings of the National Academy of Sciences of the United States of America, 93*(13), 6830–6834, https://doi.org/10.1073/pnas.93.13.6830.

Li, R. W., Ngo, C., Nguyen, J., & Levi, D. M. (2011). Video-game play induces plasticity in the visual system of adults with amblyopia. *PLoS Biology, 9*(8), e1001135, https://doi.org/10.1371/journal.pbio.1001135.

Liu, X. Y., & Zhang, J. Y. (2018). Dichoptic training in adults with amblyopia: Additional stereoacuity gains over monocular training. *Vision Research, 152*, 84–90, https://doi.org/10.1016/j.visres.2017.07.002.

Liu, X. Y., & Zhang, J. Y. (2019). Dichoptic de-masking learning in adults with amblyopia and its mechanisms. *Investigative Ophthalmology Visual Science, 60*(8), 2968–2977, https://doi.org/10.1167/iovs.18-26483.

Liu, Z. L. (1999). Perceptual learning in motion discrimination that generalizes across motion directions. *Proceedings of the National Academy of Sciences of the United States of America, 96*(24), 14085–14087, https://doi.org/10.1073/pnas.96.24.14085.

Lu, Z. L., & Dosher, B. A. (2022). Current directions in visual perceptual learning. *Nature Reviews. Psychology, 1*(11), 654–668, https://doi.org/10.1038/s44159-022-00107-2.

Lu, Z. L., Lin, Z. C., & Dosher, B. A. (2016). Translating perceptual learning from the laboratory to applications. *Trends in Cognitive Sciences, 20*(8), 561–563, https://doi.org/10.1016/j.tics.2016.05.007.

Manenti, G. L., Dizaji, A. S., & Schwiedrzik, C. M. (2023). Variability in training unlocks generalization

in visual perceptual learning through invariant representations. *Current Biology, 33*(5), 817–826.e813, https://doi.org/10.1016/j.cub.2023.01.011.

Maniglia, M., Pavan, A., Sato, G., Contemori, G., Montemurro, S., Battaglini, L., . . . Casco, C. (2016). Perceptual learning leads to long lasting visual improvement in patients with central vision loss. *Restorative Neurology and Neuroscience, 34*(5), 697–720, https://doi.org/10.3233/Rnn-150575.

Maniglia, M., & Seitz, A. R. (2018). Towards a whole brain model of perceptual learning. *Current Opinion in Behavioral Sciences, 20*, 47–55, https://doi.org/10.1016/j.cobeha.2017.10.004.

McGovern, D. P., Webb, B. S., & Peirce, J. W. (2012). Transfer of perceptual learning between different visual tasks. *Journal of Vision, 12*(11), 4, https://doi.org/https://doi.org/10.1167/12.11.4.

Nahum, M., Nelken, I., & Ahissar, M. (2010). Stimulus uncertainty and perceptual learning: similar principles govern auditory and visual learning. *Vision Research, 50*(4), 391–401, https://doi.org/10.1016/j.visres.2009.09.004.

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision, 10*(4), 437–442, https://doi.org/10.1163/156856897x00366.

Polat, U., Ma-Naim, T., & Spierer, A. (2009). Treatment of children with amblyopia by perceptual learning. *Vision Research, 49*(21), 2599–2603, https://doi.org/10.1016/j.visres.2009.07.008.

Polat, U., Schor, C., Tong, J. L., Zomet, A., Lev, M., Yehezkel, O., . . . Levi, D. M. (2012). Training the brain to overcome the effect of aging on the human eye. *Scientific Reports, 2*, https://doi.org/10.1038/srep00278.

Poletiek, F. H., & van Schijndel, T. J. P. (2009). Stimulus set size and statistical coverage of the grammar in artificial grammar learning [Article]. *Psychonomic Bulletin & Review, 16*(6), 1058–1064, https://doi.org/10.3758/pbr.16.6.1058.

Raviv, L., Lupyan, G., & Green, S. C. (2022). How variability shapes learning and generalization. *Trends in Cognitive Sciences, 26*(6), 462–483, https://doi.org/10.1016/j.tics.2022.03.007.

Sagi, D. (2011). Perceptual learning in vision research. *Vision Research, 51*(13), 1552–1566, https://doi.org/10.1016/j.visres.2010.10.019.

Schiff, R., Ashkenazi, P., Kahta, S., & Sasson, A. (2021). Stimulus variation-based training enhances artificial grammar learning [Article]. *Acta Psychologica, 214*, 103252, https://doi.org/10.1016/j.actpsy.2021.103252.

Schoups, A., Vogels, R., Qian, N., & Orban, G. (2001). Practising orientation identification

improves orientation coding in V1 neurons. *Nature, 412*(6846), 549–553, https://doi.org/10.1038/35087601.

Schoups, A. A., Vogels, R., & Orban, G. A. (1995). Human perceptual learning in identifying the oblique orientation: Retinotopy, orientation specificity and monocularity. *Journal of Physiology, 483*(Pt 3), 797–810, https://doi.org/10.1113/jphysiol.1995.sp020623.

Sterkin, A., Yehezkel, O., Bonneh, Y. S., Norcia, A., & Polat, U. (2009). Backward masking suppresses collinear facilitation in the visual cortex. *Vision Res, 49*(14), 1784–1794, https://doi.org/10.1016/j.visres.2009.04.013.

Tartaglia, E. M., Aberg, K. C., & Herzog, M. H. (2009). Perceptual learning and roving: Stimulus types and overlapping neural populations [Research Support, Non-U.S. Gov't]. *Vision Research, 49*(11), 1420–1427, https://doi.org/10.1016/j.visres.2009.02.013.

Teich, A. F., & Qian, N. (2003). Learning and adaptation in a recurrent model of V1 orientation selectivity. *Journal of Neurophysiology, 89*(4), 2086–2100, https://doi.org/10.1152/jn.00970.2002.

Tenebaum, J. B., & Griffiths, T. L. (2001). Generalization, similarity, and Bayesian inference [Article]. *Behavioral and Brain Sciences, 24*(4), 629–+, https://doi.org/10.1017/s0140525x01000061.

Travlos, A. K. (2010). Specificity and variability of practice, and contextual interference in acquisition and transfer of an underhand volleyball serve. *Perceptual and Motor Skills, 110*(1), 298–312, https://doi.org/10.2466/PMS.110.1.298-312.

Vlach, H. A., & Sandhofer, C. M. (2012). Distributing learning over time: The spacing effect in children's acquisition and generalization of science concepts. *Child Development, 83*(4), 1137–1144, https://doi.org/10.1111/j.1467-8624.2012.01781.x.

Vlach, H. A., Sandhofer, C. M., & Kornell, N. (2008). The spacing effect in children's memory and category induction. *Cognition, 109*(1), 163–167, https://doi.org/10.1016/j.cognition.2008.07.013.

Vogels, R. (2023). Perceptual learning: Breaking specificity by variability. *Current Biology, 33*(5), R182–R185, https://doi.org/10.1016/j.cub.2023.01.025.

Wang, R., Cong, L. J., & Yu, C. (2013). The classical TDT perceptual learning is mostly temporal learning. *Journal of Vision, 13*(5), 1–9, https://doi.org/Artn 910.1167/13.5.9.

Wang, R., Wang, J., Zhang, J. Y., Xie, X. Y., Yang, Y. X., Luo, S. H., . . . Li, W. (2016). Perceptual learning at a conceptual level.

Journal of Neuroscience, 36(7), 2238–2246, https://doi.org/10.1523/JNEUROSCI.2732-15.2016.

Wang, R., Zhang, J. Y., Klein, S. A., Levi, D. M., & Yu, C. (2012). Task relevancy and demand modulate double-training enabled transfer of perceptual learning. *Vision Research, 61*, 33–38, https://doi.org/10.1016/j.visres.2011.07.019.

Wang, R., Zhang, J. Y., Klein, S. A., Levi, D. M., & Yu, C. (2014). Vernier perceptual learning transfers to completely untrained retinal locations after double training: A "piggybacking" effect. *Journal of Vision, 14*(13), 12, https://doi.org/10.1167/14.13.12.

Watanabe, T., & Sasaki, Y. (2015). Perceptual learning: Toward a comprehensive theory. *Annual Review of Psychology, 66*, 197–221, https://doi.org/10.1146/annurev-psych-010814-015214.

Wenliang, L. K., & Seitz, A. R. (2018). Deep neural networks for modeling visual perceptual learning. *Journal of Neuroscience, 38*(27), 6028–6044, https://doi.org/10.1523/Jneurosci.1620-17.2018.

Xiao, L. Q., Zhang, J. Y., Wang, R., Klein, S. A., Levi, D. M., & Yu, C. (2008). Complete transfer of perceptual learning across retinal locations enabled by double training. *Current Biology, 18*(24), 1922–1926, https://doi.org/10.1016/j.cub.2008.10.030.

Xie, X.-Y., & Yu, C. (2020). A new format of perceptual learning based on evidence abstraction from multiple stimuli. *Journal of Vision, 20*(2), 5, https://doi.org/10.1167/jov.20.2.5.

Xiong, Y.-Z., Guan, S.-C., & Yu, C. (2022). A supramodal and conceptual representation of subsecond time revealed with perceptual learning of temporal interval discrimination. *Scientific Reports, 12*(1), 10668, https://doi.org/10.1038/s41598-022-14698-6.

Xiong, Y. Z., Xie, X. Y., & Yu, C. (2016). Location and direction specificity in motion direction learning associated with a single-level method of constant stimuli. *Vision Research, 119*, 9–15, https://doi.org/10.1016/j.visres.2015.11.005.

Xiong, Y. Z., Zhang, J. Y., & Yu, C. (2016). Bottom-up and top-down influences at untrained conditions determine perceptual learning specificity and transfer. *Elife, 5*, e14614, https://doi.org/10.7554/eLife.14614.

Xu, F., & Tenenbaum, J. B. (2007). Word learning as Bayesian inference [Review]. *Psychological Review, 114*(2), 245–272, https://doi.org/10.1037/0033-295x.114.2.245.

Yang, T. M., & Maunsell, J. H. R. (2004). The effect of perceptual learning on neuronal responses in monkey visual area V4. *Journal of Neuroscience, 24*(7), 1617–1626, https://doi.org/10.1523/Jneurosci.4442-03.2004.

Yashar, A., & Denison, R. N. (2017). Feature reliability determines specificity and transfer of perceptual learning in orientation search. *PLoS Computational Biology, 13*(12), e1005882, https://doi.org/10.1371/journal.pcbi.1005882.

Yotsumoto, Y., Chang, L. H., Watanabe, T., & Sasaki, Y. (2009). Interference and feature specificity in visual perceptual learning. *Vision Research, 49*(21), 2611–2623, https://doi.org/10.1016/j.visres.2009.08.001.

Yu, C., Klein, S. A., & Levi, D. M. (2004). Perceptual learning in contrast discrimination and the (minimal) role of context. *Journal of Vision, 4*(3), 169–182, https://doi.org/10.1167/4.3.4.

Zhang, J. Y., Cong, L. J., Klein, S. A., Levi, D. M., & Yu, C. (2014). Perceptual learning improves adult amblyopic vision through rule-based cognitive compensation. *Investigative Ophthalmology & Visual Science, 55*(4), 2020–2030, https://doi.org/10.1167/iovs.13-13739.

Zhang, J. Y., Kuai, S. G., Xiao, L. Q., Klein, S. A., Levi, D. M., & Yu, C. (2008). Stimulus coding rules for perceptual learning. *PLoS Biology, 6*(8), e197, https://doi.org/10.1371/journal.pbio.0060197.

Zhang, J. Y., & Yang, Y. X. (2014). Perceptual learning of motion direction discrimination transfers to an opposite direction with TPE training. *Vision Research, 99*, 93–98, https://doi.org/10.1016/j.visres.2013.10.011.

Zhang, J. Y., Zhang, G. L., Xiao, L. Q., Klein, S. A., Levi, D. M., & Yu, C. (2010). Rule-based learning explains visual perceptual learning and its specificity and transfer. *Journal of Neuroscience, 30*(37), 12323–12328, https://doi.org/10.1523/JNEUROSCI.0704-10.2010.