

Feature variability determines specificity and transfer in multiorientation feature detection learning

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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 & Doshier, 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 (Doshier & 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, Doshier, Petrov, & Lu, 2009; Liu, 1999), training amount (Aberg, Tartaglia, & Herzog, 2009; Jeter, Doshier, Liu, & Lu, 2010), stimulus complexity (Bakhtiari, Awada, & Pack, 2020; McGovern, Webb, & Peirce, 2012), state of adaptation

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(Harris, Gliksberg, & Sagi, 2012), spatial attention (Donovan & Carrasco, 2018; Donovan, Szpiro, & Carrasco, 2015), training task and psychophysical methods (Green, Kattner, Siegel, Kersten, & Schrater, 2015;

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

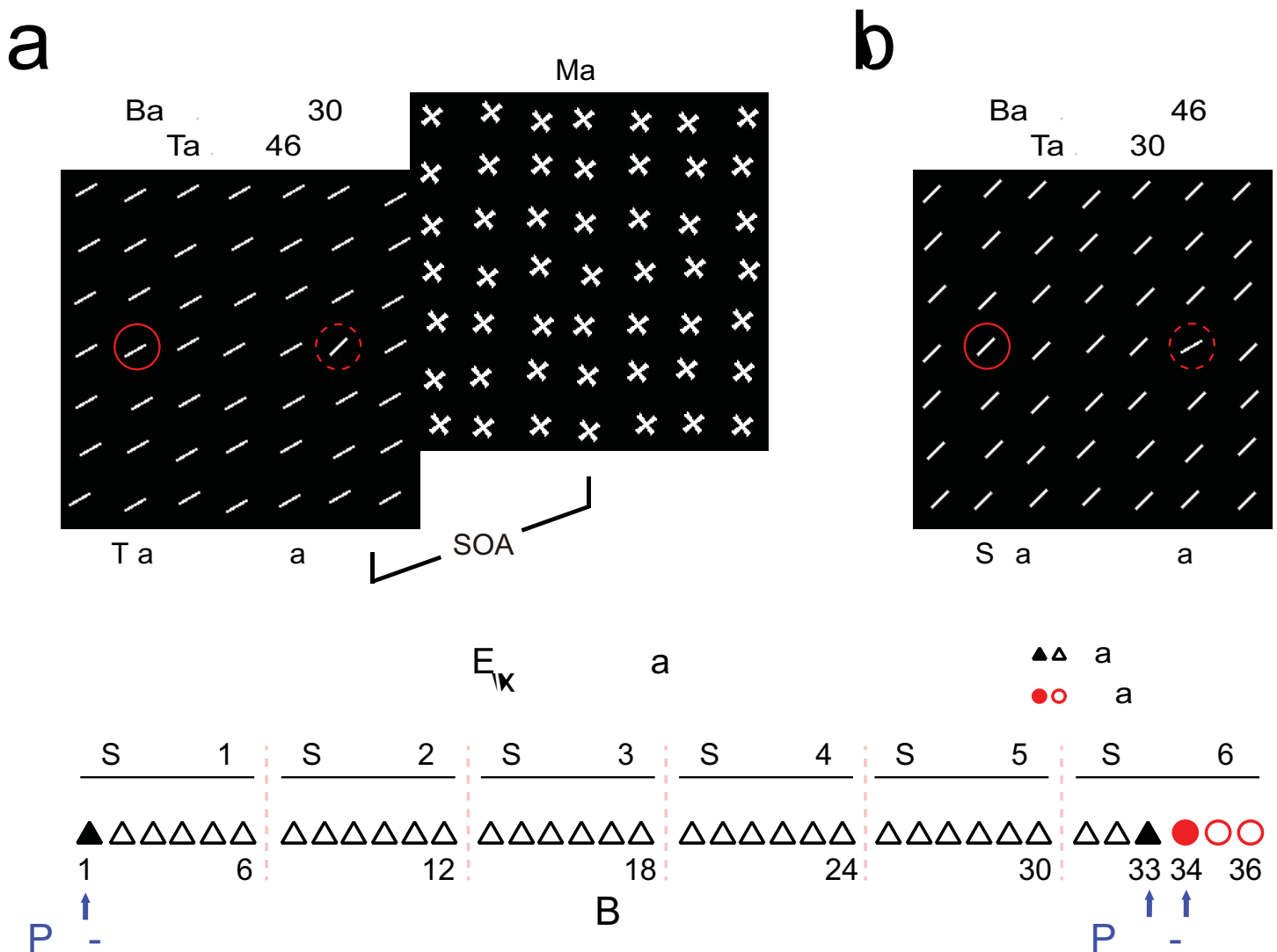


Figure 1. Stimuli and experimental schedule. (a) Stimulus configuration of the feature detection task at trained target-background orientations (46° vs 30°) and mask. The odd element (target) could appear at one of two positions (indicated by red circles that were not present in the actual stimuli). 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 1a). 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

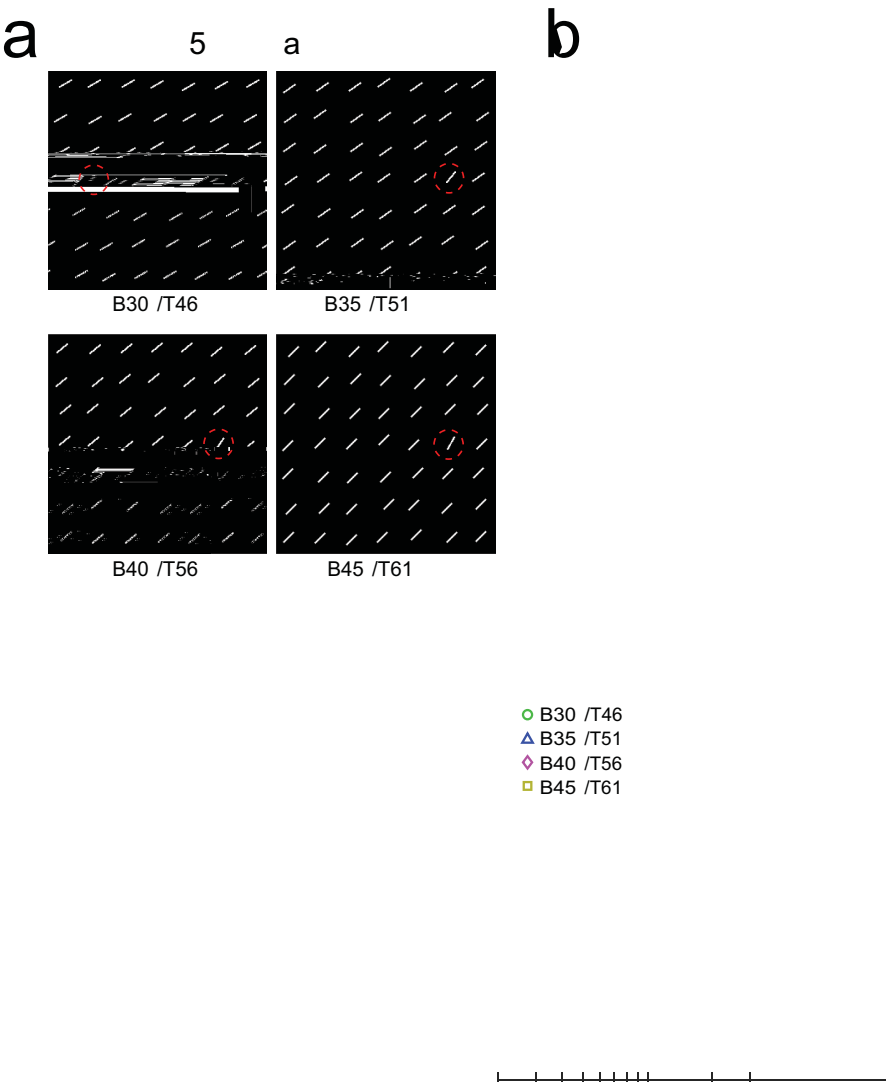
	Orientation deviation	Presentation order	Training paradigm
Condition 1	5° deviation	Roving	Training
Condition 2	45° deviation	Roving	Training
Condition 3	5° deviation	Roving	Training plus exposure
Condition 4	5° deviation	Block	Training

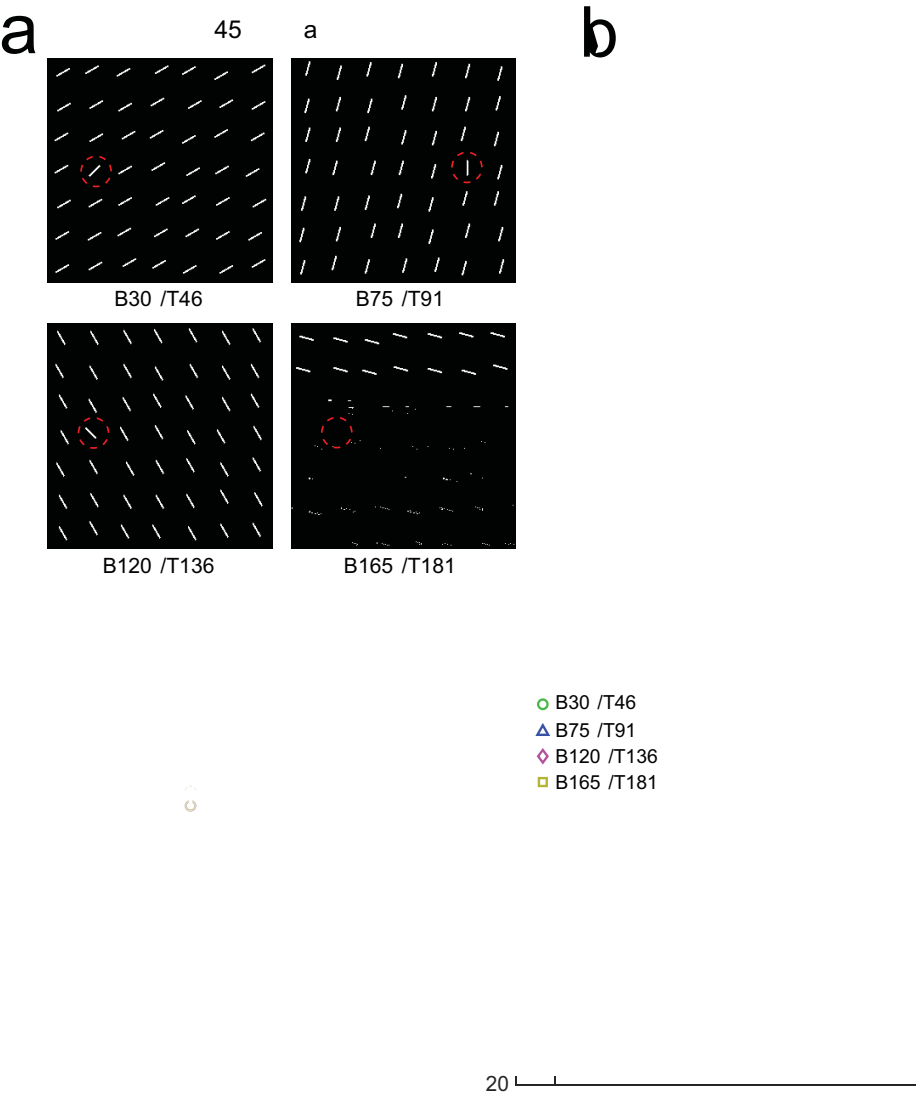
Table 1. Study design. The key differences between the four training conditions exist in the orientation deviation of the four orientation search stimuli, the presentation order of the four orientation search stimuli, and the training paradigm.

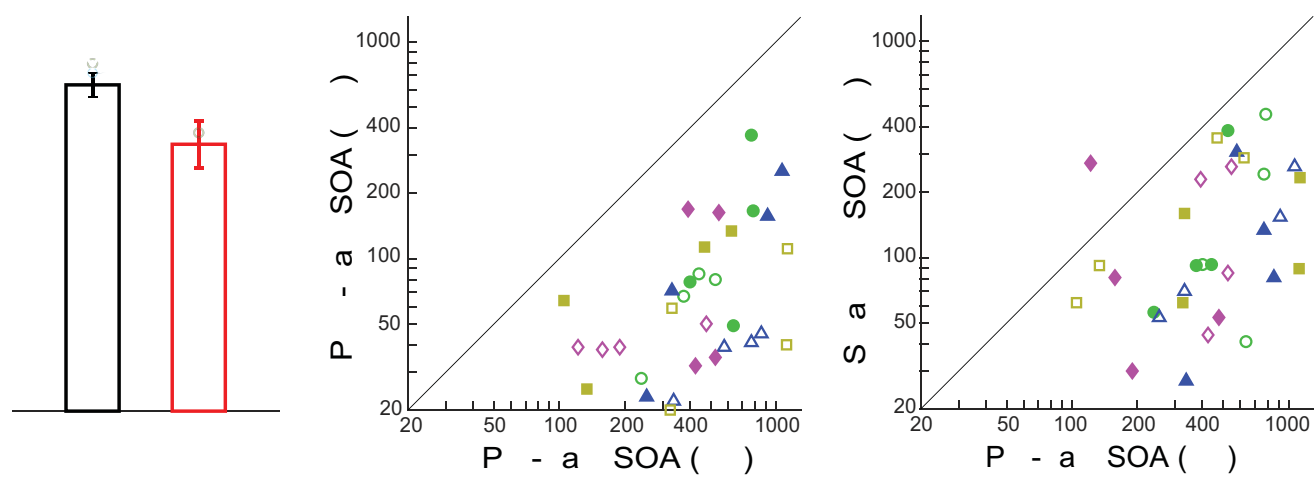
could always make a correct discrimination. The step size of the staircase was 0.05 log units. Each staircase consisted of four preliminary reversals and six experimental reversals. A reversal occurs if the stimulus value moves up when it was last moved down, or vice versa. The geometric mean of the 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 consisting of 10 trials. The training phase was conducted in a random order, with each stimulus appearing in each block. The training phase was conducted in a random order, with each stimulus appearing in each block.





b

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), $\text{MPI}_{\text{trained}} = 79.2 \pm 3.6\%$, $t_7 = 21.71$, $p < 0.001$, 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), $\text{MPI}_{\text{swapped}} = 10.5 \pm 12.7\%$, $t_7 = 0.83$, $p = 0.43$, 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), $\text{MPI}_{\text{block 36/block 34}} = 30.8 \pm 12.7\%$, $t_7 = 2.43$, $p = 0.046$, Cohen's $d = 0.86$; in contrast, the initial training of the trained orientations at the first three blocks produced fewer improvements, $\text{MPI}_{\text{block 3/block 1}} = 8.9 \pm 12.4\%$, $t_7 = 0.71$, $p = 0.50$, 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), $\text{MPI}_{\text{trained}} = 73.4 \pm 1.9\%$, $t_7 = 39.49$, $p < 0.001$, 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 multi-stimulus learning. The threshold improvements of swapped orientations were also significantly different from zero (Figure 3c), $\text{MPI}_{\text{swapped}} = 68.3 \pm 5.4\%$, $t_7 = 12.63$, $p < 0.001$, 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), $\text{MPI}_{\text{block 36/block 34}} = 11.0 \pm 10.4\%$, $t_7 = 1.06$, $p = 0.33$, 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., $B91^\circ/T75^\circ$ or $B181^\circ/T165^\circ$) was more efficient than the reverse scenario (e.g., $B75^\circ/T91^\circ$ or $B165^\circ/T181^\circ$), as the orientation search asymmetry reported by Yashar and Denison (2017). Specifically, three observers trained with $B91^\circ/T75^\circ$ or $B181^\circ/T165^\circ$ showed little transfer to the swapped situations $B75^\circ/T91^\circ$ or $B165^\circ/T181^\circ$, $\text{Threshold}_{\text{pre}_B91^\circ/T75^\circ} = 254.7 \pm 27.8$ ms, $\text{Threshold}_{\text{post}_B91^\circ/T75^\circ} = 57.0 \pm 10.4$ ms, $\text{Threshold}_{\text{swapped}_B75^\circ/T91^\circ} = 189.7 \pm 49.7$ ms; $\text{Threshold}_{\text{pre}_B181^\circ/T165^\circ} = 410.0 \pm 142.1$ ms, $\text{Threshold}_{\text{post}_B181^\circ/T165^\circ} = 54.3 \pm 18.8$ ms, $\text{Threshold}_{\text{swapped}_B165^\circ/T181^\circ} = 400.0 \pm 42.6$ ms. Conversely, five observers trained with $B75^\circ/T91^\circ$ or $B165^\circ/T181^\circ$ showed complete transfer to the swapped situations $B91^\circ/T75^\circ$ or $B181^\circ/T165^\circ$, $\text{Threshold}_{\text{pre}_B75^\circ/T91^\circ} = 491.3 \pm 66.3$ ms, $\text{Threshold}_{\text{post}_B75^\circ/T91^\circ} = 199.2 \pm 37.9$ ms, $\text{Threshold}_{\text{swapped}_B91^\circ/T75^\circ} = 118.9 \pm 37.4$ ms; $\text{Threshold}_{\text{pre}_B165^\circ/T181^\circ} = 793.0 \pm 205.4$ ms,

$\text{Threshold}_{\text{post_B165}^\circ/\text{T181}^\circ} = 185.6 \pm 52.0$ ms, $\text{Threshold}_{\text{swapped_B181}^\circ/\text{T165}^\circ} = 118.2 \pm 36.2$ 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, $\text{MPI}_{5^\circ \text{ deviation}} = 78.4 \pm 1.3\%$, $\text{MPI}_{\text{trained}} = 72.7 \pm 2.1\%$, $t_3 = 2.18$, $p = 0.12$, 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

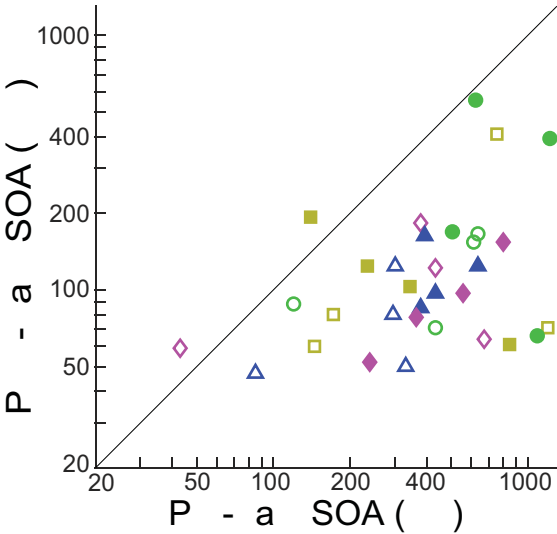
were bars (uniformly oriented at the background orientations without the odd element presented in 80% of trials) or circles (20% of trials) in each 60-trial block (Figure 4a). The TPE procedure was performed in the same session from the second to the fifth session. Changes in block-by-block SOA thresholds 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), $\text{MPI}_{\text{trained}} = 83.4 \pm 3.1\%$; $t_7 = 26.70$, $p < 0.001$, 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), $\text{MPI}_{\text{swapped}} = 68.3 \pm 5.9\%$, $t_7 = 11.48$, $p < 0.001$, 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), $\text{MPI}_{\text{block 36/block 34}} = 12.4 \pm 8.9\%$, $t_7 = 1.40$, $p = 0.21$, Cohen's $d = 0.49$, suggesting substantial learning transfer to the swapped orientations has occurred after the TPE training.

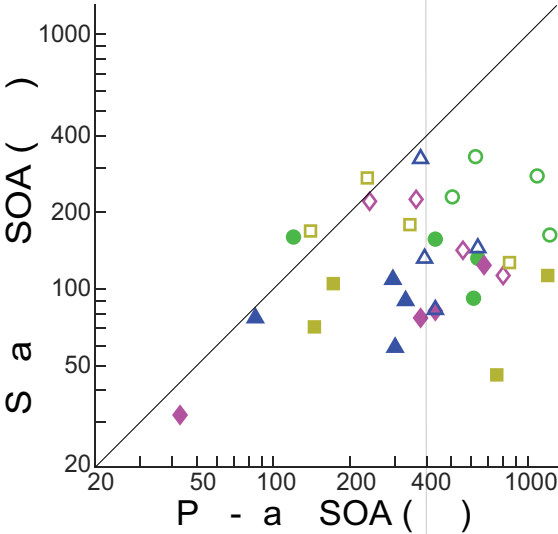
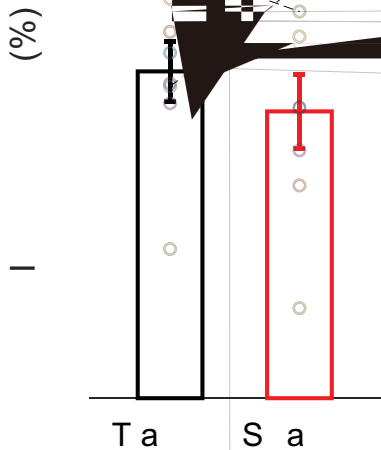
Condition 4: Perceptual learning of four orientation search stimuli with a 5° deviation in a blocked condition

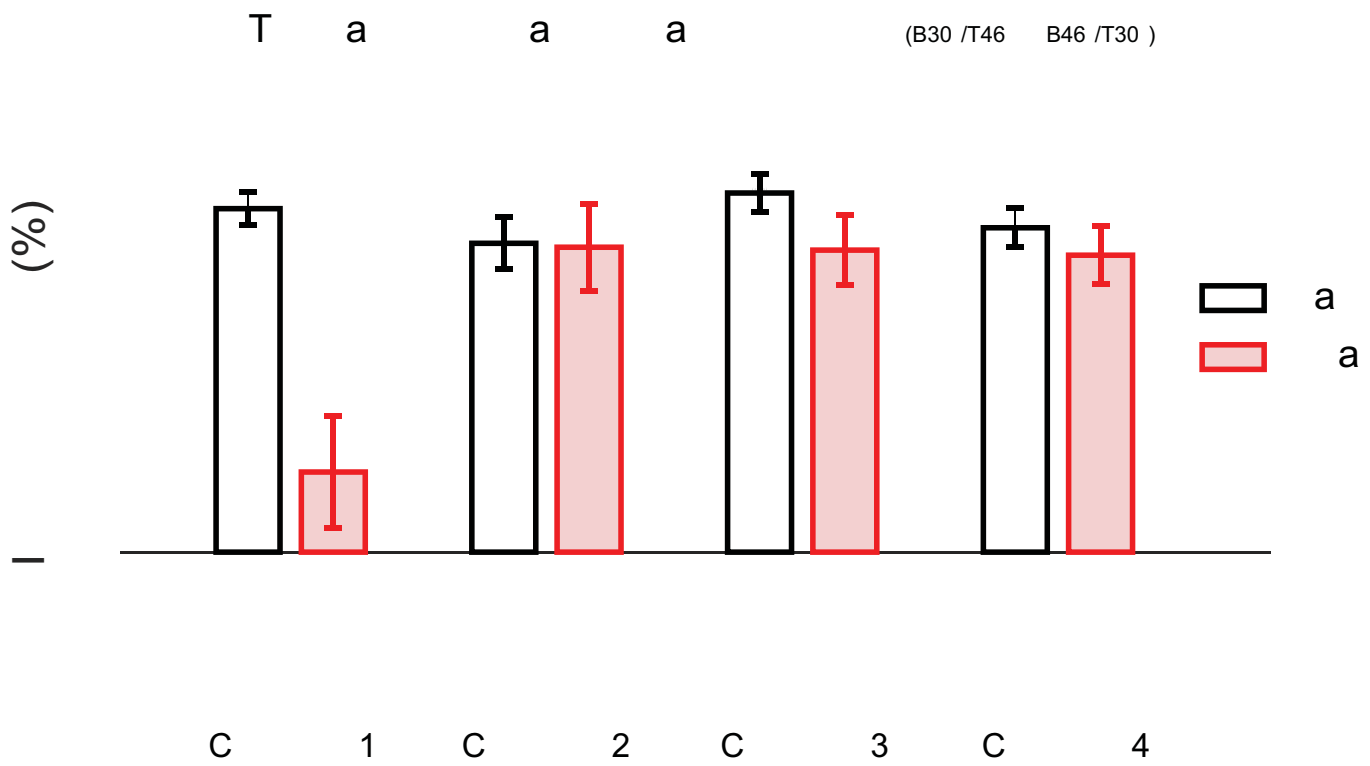
Previous studies have shown that learning occurred when multiple stimuli were presented in a fixed order, but not in a random order (roving) (Kuai et al., 2005; Yu, Klein, & Levi, 2004; Zhang et al., 2008). In addition, it has been shown that training schedules, such as when learning from the same examples, 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

a



b





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, Bonne, 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

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, & Doshier, 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

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