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Location and direction specificity in motion direction learning associated with a single-level method of constant stimuli



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ABSTRACT

Recent studies reported significantly less location specificity in motion direction learning than in previous classical studies. The latter performed training with the method of constant stimuli containing a single level of direction difference. In contrast the former used staircase methods that varied the direction difference trial by trial. We suspect that extensive practice with a single direction difference could allow an observer to use some subtle local cues for direction discrimination. Such local cues may be unavailable at a new stimulus location, leading to higher location specificity. To test this hypothesis, we jittered slightly the directions of a stimulus pair by the same amount while keeping the direction difference constant, so as to disturb the potential local cues. We observed significantly more transfer of learning to untrained locations. The local cue effects may also explain the recent controversies regarding the finding that foveal motion direction learning becomes significantly more transferrable to a new direction with TPE (training-plus-exposure) training. One specific study by Zili Liu and collaborators that challenges this finding also used a single-level direction difference for training. We first replicated their results. But we found that if the directions of the stimulus pair were again jittered while the direction difference was kept constant, motion direction learning transferred significantly more to an orthogonal direction with TPE training. Our results thus demonstrate the importance of using appropriate psychophysical methods in training to reduce local-cue related specificity in perceptual learning.

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1. Introduction

Visual perceptual learning improves a person's sensitivity to fine differences of basic visual features, such as spatial frequency, orientation, contrast, and motion direction (Ahissar & Hochstein, 1997; Ball & Sekuler, 1982, 1987; Doshier & Lu, 1998; Fiorentini & Berardi, 1980; Schoups, Vogels, & Orban, 1995; Shiu & Pashler, 1992; Yu, Klein, & Levi, 2004). Like various VPL tasks, motion direction learning is found to be specific to the trained retinal location and feature dimension (i.e., a specific direction), which has led to the assumption that motion direction learning may suggest training-altered response properties of direction-selective visual neurons (Ball & Sekuler, 1982, 1987). However, neurophysiologically motion direction learning is more likely tied to changes in non-sensory cortical areas like LIP, and in contrast no significant changes of response properties of MT neurons are recorded (Law & Gold, 2008). Hence it is inferred that motion direction learning

may more likely depend on a reweighting mechanism, in that training improves the readout of sensory inputs from direction selective neurons at a decision level (Law & Gold, 2009).

The understanding of the mechanisms underlying motion direction learning is further advanced by two recent developments. The first development is that, in contrast to the strong location specificity first reported in the classical studies of Ball and Sekuler (1982, 1987), more significant learning transfer to untrained quadrant/hemisphere locations is observed (Wang, Zhang, Klein, Levi, & Yu, 2014; Zhang & Li, 2010). When gauged with a transfer index (TI) as the ratio of transfer/learning, TI is about 0.2 in Ball and Sekuler (1982, 1987), but it is significantly higher at 0.65 in Zhang and Li (2010) and 0.77 in Wang et al. (2014). This learning transfer, especially across brain hemispheres, is consistent with the neurophysiological data that motion direction learning may primarily occur in high-level non-sensory brain areas. A second development is that the direction specificity in motion direction learning, first reported by Ball and Sekuler (1982, 1987), can be minimized with a new training-plus-exposure (TPE) experimental design (Zhang & Yang, 2014). Specifically, motion direction learning transfers significantly to an opposite direction if the observers

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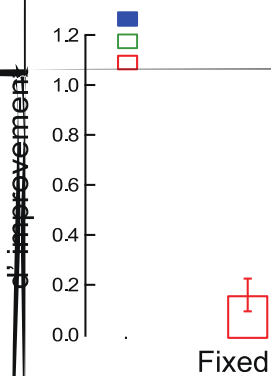
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are additionally exposed to the untrained opposite direction through an irrelevant dot-number discrimination task (Zhang & Yang, 2014). These observations of learning transfer to untrained quadrants or hemisphere and directions suggest that motion direction learning is not just a reweighting process in which the brain learns to better read out the direction inputs from specific neurons activated by the trained stimuli. Rather motion direction learning is a smarter process in which the brain learns the rules of reweighting, so that these rules can be applied to new direction signals from untrained locations and directions to improve motion direction discrimination.

We conducted the current study to address two issues arising from the above developments. First, we wanted to find out why motion direction learning is less location specific in recent studies as compared to Ball and Sekuler's classical work. Second, the TPE-enabled transfer of motion direction learning to untrained directions is challenged in two papers by Zili Liu and collaborators (Liang, Zhou, Fahle, and Liu (2015a, 2015b)). In this study we mainly address one paper (Liang et al., 2015a) and lightly touch the other one (Liang et al., 2015b) that we will fully address in a separate article. Liang et al. (2015a) reported no significant learning transfer with TPE training, in which the observers first practiced motion direction discrimination for 23 days, and then they were exposed to an orthogonal direction via practicing a contrast discrimination task at the orthogonal direction for another 23 days. Although Liang et al. (2015a) concluded that long-term multiple-week training may fail the TPE effects, our experiments actually replicated their data with short-term 5-day TPE training (see Section 3). However, we noticed that both Ball and Sekuler (1982, 1987) and Liang et al. (2015a) used a special format of the method of constant stimuli in their training. Specifically, only one level of direction difference, which was defined by a pair of fixed motion stimuli, was used to train the observers, and the amount of learning and transfer was indexed by the d' changes (from now on we call this the single-interval MCS method). In contrast, the recent studies (Wang et al., 2014; Zhang & Li, 2010; Zhang & Yang, 2014) used staircase methods to train the observers.

The single-level MCS method and the staircase method differ in an important way that could potentially alter the transfer effects. The single-level MCS method presents the stimuli at a single direction difference that is defined by a pair of fixed stimuli. However, the staircase method is a self-adaptive procedure in which the direction difference keeps changing, and so do the stimuli defining the direction differences. We suspect that when the single-level MCS method is used, the observers may learn to use some subtle local cues that are specific to the fixed stimuli to help the motion direction judgments. Mollon and Danilova (1996) interpreted these local cues as "the local idiosyncracies of his retinal image, of his receptor mosaic". One potential local cue may be related to the



The foveal motion stimuli were also identical to those used in another previous study (Zhang & Yang, 2014) except that the stimulus duration was slightly different. Each foveal presentation consisted of 400 white random dots (3×3 pixels each at the maximum luminance). These dots appeared in an invisible 8° -diameter (minimal luminance) circular window centered on a black background. All dots moved in the same direction at a speed of 1 pixel/ms. Each dot had a lifetime of 0–300 ms depending on its starting position. When a dot reached its lifetime, a new dot emerged from a random position within the stimulus window. When a dot moved out of the stimulus window, a new dot entered from the opposite side of the window at a random position.

2.3. Procedure

2.3.1. Peripheral motion direction discrimination

Each 2AFC trial consisted of two 500-ms stimulus intervals that were separated by a 500-ms inter-stimulus interval. A small

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“same” and “different” trials were randomly mixed in the experiments.

In pre- and post-training sessions, d' was measured at the trained quadrant location plus two of three untrained quadrant locations that were randomly assigned to an observer. Each location was tested for 5 blocks of trials (50 trials per block). Training sessions were conducted in separate days, each consisting of 16 blocks and lasted for approximately 1.5 h.

2.3.2. Foveal motion direction discrimination and dot-number discrimination

The foveal tasks included motion direction discrimination and dot-number discrimination, both measured with a staircase method or a single-level MCS method in difference experimental conditions. In a trial, a fixation point appeared 350 ms before the stimulus onset and stayed through the trial. The two 500-ms stimulus intervals were separated by a 200 ms inter-stimulus interval. In a direction discrimination task, the observers reported which stimulus direction was more clockwise (staircase measurement), or whether the two directions were the same or different (single-level MCS measurement). In a dot-number discrimination task, they reported which stimulus interval contained more dots (staircase measurement), or whether the two intervals contained the same or different number of dots (single-level MCS measurement).

The staircase measures followed a 3-down-1-up rule with a 0.05 log unit step size. Each staircase consisted of four preliminary reversals and six experimental reversals (50–60 trials). The geometric mean of the experimental reversals was taken as the threshold. The single-level MCS method measured d' of every 50-trial block. In a motion direction discrimination task the two motion directions were either identical at a reference direction or different by 3° at reference direction $\pm 1.5^\circ$ for all participating observers. The reference direction was 22.5° or 112.5° when not jittered. In a dot number discrimination task the two moving stimuli contained different numbers (400 vs. 250) of dots.

In pre- and post-training sessions, motion direction discrimination at each trained or transfer directions was tested with 5 staircases (50–60 trials per staircase) or 5 blocks of trials (50 trials per block). The training sessions were conducted in separate days. Each training session consisted of 20 staircases or blocks of trials and lasted for approximately 1.5 h.

3. Results

3.1. Part I: Location specificity in motion direction learning associated with single-level MCS training

We first replicated the classical findings of strong location specificity of motion direction learning with the single-level MCS training method (Ball & Sekuler, 1982, 1987). Five sessions of practice improved d' by 0.81 ± 0.11 at a trained location ($p < 0.001$; two-tailed paired t-test), suggesting significant motion direction learning. Moreover, d' for the same stimulus was significantly improved at an untrained ipsilateral quadrant location ($\Delta d' = 0.66 \pm 0.16$, $p = 0.009$), showing great learning transfer (see discussion later for possible explanations). However, there was much less d' changes at the untrained diagonal quadrant location ($\Delta d' = 0.18 \pm 0.07$, $p = 0.029$) and contralateral quadrant location ($\Delta d' = 0.23 \pm 0.09$, $p = 0.053$), showing less learning transfer and more location specificity (Fig. 1b and e).

Since we suspected that at least part of the location specificity might be attributed to local cue learning, we jittered the stimulus directions trial by trial within a range of $\pm 4^\circ$ during five training sessions. Here the two stimulus directions of a 2AFC trial were equally changed by direction jitter, so that the direction difference

remained fixed. In addition, the stimulus directions were not jittered in the pre- and post-training sessions, so that the learning and transfer effects could be compared between jittered and fixed direction training experiments. Training improved d' by 0.97 ± 0.10 at the trained location ($p < 0.001$), and nearly equally by 0.94 ± 0.14 at an untrained ipsilateral location ($p < 0.001$). Consistent with our prediction, more improvement was evident at untrained diagonal location ($\Delta d' = 0.56 \pm 0.09$, $p < 0.001$) and contralateral location ($\Delta d' = 0.67 \pm 0.13$, $p = 0.002$) (Fig. 1c and e) than those in the earlier fixed training experiment.

The direction jitter effects are better appreciated with the scatter plots in Fig. 1d where individual data in fixed and jittered direction conditions are plotted together for each trained or transfer retinal quadrants, respectively. The empty dots (fixed directions) and filled dots (jittered conditions), all above the diagonal line to show d' improvement, overlap at the trained location as well as the ipsilateral quadrant location. These results suggest similar learning effects and similar learning transfer to the ipsilateral quadrant location. At the diagonal and contralateral quadrant locations, the filled dots tend to be more above the diagonal line than the empty dots, indicating that jittered direction condition produces more learning transfer than does the fixed condition.

To quantitatively compare learning transfer or location specificity between jittered and fixed direction conditions, we calculated the transfer index (TI) as $\Delta d'_{\text{untrained}}/\Delta d'_{\text{trained}}$ for each condition (Fig. 1f). The TI values were 0.80 ± 0.20 for the ipsilateral location, 0.25 ± 0.09 for the diagonal location, and 0.27 ± 0.06 for the contralateral location in the fixed direction condition, and were 0.98 ± 0.08 for the ipsilateral location, 0.63 ± 0.13 for the diagonal location, and 0.65 ± 0.10 for the contralateral location in the jittered direction condition. Since learning transfer to an ipsilateral location was nearly complete in both conditions, we were only interested in the performance changes at diagonal and contralateral locations. A two-way ANOVA of the transfer index data with Group (fixed vs. jittered) and Location (diagonal vs. contralateral) as two factors showed a significant main effect of Group ($F(1, 26) = 12.69$, $p = 0.001$), but an insignificant main effect of Location ($F(1, 26) = 0.04$, $p = 0.843$). These results indicate that the direction jitter significantly increased learning transfer to two untrained locations by a similar amount, consistent with the local-cue learning hypothesis.

3.2. Part II. Direction specificity and TPE-enabled transfer in motion direction learning: The possible roles of local-cue learning

We first verified the finding that TPE training fails to enable transfer of motion direction learning to an orthogonal direction when training is performed with a single-level MCS method (Liang et al., 2015a). Although the authors claim that long-term training minimizes TPE-enabled learning transfer, the Liang et al. (2015a) differs from Zhang and Yang (2014) in two important ways, not only the training lengths but also the psychophysical methods (single-level MCS method vs. staircase method). Therefore, instead of 23 days of training plus 23 days of exposure in Liang et al. (2015a), we shortened the length of TPE training to 5 days to test whether the training length really mattered in Liang et al. (2015a). Here the training and exposure tasks in a TPE experimental design were interleaved in alternating blocks of trials within the same sessions. Previous evidence has shown that simultaneous and sequential TPE trainings both produce significant learning transfer with a staircase method (Zhang & Yang, 2014).

Six observers in a baseline condition practiced foveal motion direction training with the single-level MCS method at either 22.5° or 112.5° reference directions for 5 sessions, which improved d' by 0.98 ± 0.08 ($p < 0.001$, Fig. 2b and d). However, learning did

not transfer much to an orthogonal direction ($\Delta d' = 0.26 \pm 0.17$, $p = 0.18$, Fig. 2b and d), with $TI = 0.23 \pm 0.15$ (Fig. 2e), replicating the known direction specificity in motion direction learning. Another eight observers learned the same task in a TPE design. These observers not only practiced motion direction discrimination as in the baseline condition, but they also received exposure to the orthogonal transfer direction via performing an irrelevant dot-number discrimination task in which the dot stimuli were moving at the orthogonal direction, in alternating blocks of trials. The training only lasted for 5 sessions. This short version of TPE training improved d' by 1.06 ± 0.11 ($p < 0.001$, Fig. 2c and d) at the trained directions, but not much learning transferred to the exposed orthogonal directions ($\Delta d' = 0.32 \pm 0.16$, $p = 0.08$). The $TI = 0.25 \pm 0.16$, almost identical to the TI in the baseline condition. These data confirm that TPE training with the single-level MCS method is unable to induce significant learning transfer to an untrained orthogonal direction, regardless of how long the training takes.

Next we tested the hypothesis that this failure of learning transfer may result from local-cue learning with the single-level MCS training method. We jittered the stimulus directions within a range of $\pm 2^\circ$ in training sessions while keeping the direction difference constant to disturb possible local cues. In the baseline condition, training improved d' by 1.10 ± 0.13 ($p < 0.001$, Fig. 2f and h), but the d' improvement was only 0.38 ± 0.12 at the untrained orthogonal direction with the $TI = 0.32 \pm 0.09$, showing largely direction specificity. Therefore, the disturbance of local cues with direction jitters appeared not sufficient to enable very significant transfer of foveal direction learning to an orthogonal direction. However, TPE training in another group of observers improved d' not only at the trained direction by 0.99 ± 0.22 ($p = 0.007$, Fig. 2g and h), but also at an orthogonal direction by 0.71 ± 0.16 ($p = 0.008$, Fig. 2g and h), producing less direction specificity and more learning transfer ($TI = 0.82 \pm 0.24$). In fact the d' improvements were not statistically different between the trained and the orthogonal transfer directions ($p = 0.30$, Fig. 2h). Again these data are consistent with our hypothesis that local-cue learning may affect TPE-enabled learning transfer when the single-level MCS method is used. However, in this foveal motion direction case, direction jittering is a necessary, but not a sufficient, condition for learning transfer to an orthogonal direction (see Section 4).

3.3. A supplemental experiment: TPE enabled transfer of direction learning with staircase training

In a second paper by Zili Liu and collaborators that challenges the findings of Zhang and Yang (2014), Liang et al. (2015b) reported that they failed to replicate the original data in Zhang and Yang (2014) even when an identical staircase method was used. However, a careful examination of their replicating results (their Fig. 2) indicates that their results are actually not very different from those reported in Zhang and Yang (2014). Among the six observers in their Fig. 2, one observer showed negative transfer ($TI = -0.71$), while the other five showed significant transfer (TI : mean = 0.71 ± 0.11 , range = $[0.44 \ 1.00]$), including two showing complete learning transfer ($TIs = 0.94 \ \& \ 1.00$). We will present a more detailed analysis of Liang et al. (2015b) in a separate article.

To further clarify the issue, here we also replicated the TPE training experiment in Zhang and Yang (2014) with a staircase method. The training procedures were identical to those in Zhang and Yang (2014), except that the transfer direction was orthogonal instead of opposite to the trained direction to be consistent with the current study.

The baseline plot (Fig. 3a) was actually from unpublished data of Zhang and Yang (2014) that also tested learning transfer to an orthogonal direction. The staircase training reduced the thresholds

of motion direction discrimination by $40.0 \pm 5.5\%$ ($p < 0.001$, Fig. 3a and c) at the trained direction. However, the threshold changes at an untrained orthogonal direction were small and insignificant by $9.6 \pm 8.7\%$ ($p = 0.32$, Fig. 3a and c), showing direction specificity of learning.

We then performed TPE training with another group of observers, which again involved original motion direction training and additional exposure to the transfer direction via a dot-number discrimination task. Training reduced direction thresholds at the trained direction by $48.4 \pm 4.4\%$ ($p < 0.001$, Fig. 3b and c). The thresholds at the untrained orthogonal direction were also significantly improved by $37.9 \pm 6.9\%$ ($p = 0.002$, Fig. 3b and c). There was no significant difference of threshold improvements between the trained and orthogonal directions ($p = 0.20$, Fig. 3c). The TI was 0.80 ± 0.16 , within the range of 0.62 and 1.2 TI values in Zhang and Yang (2014). These new results thus replicated the finding of Zhang and Yang (2014) that TPE training can enable significant, and sometimes complete, transfer of motion direction learning to untrained directions.

4. Discussion

Our results show that motion direction learning obtained with single-level MCS training has limited transfer to diagonal and contralateral quadrants, similar to the classical reports (Ball & Sekuler, 1982, 1987). Motion direction learning obtained with single-level MCS training also has limited transfer to an untrained transfer direction even after observers' exposure to the transfer direction via an irrelevant task in a TPE experimental design. However, jittering the stimulus directions while keeping the direction difference constant significantly reduces location specificity. It also significantly reduces direction specificity with TPE training. These results are consistent with our hypothesis that local-cue learning associated with single-level MCS training may be responsible for part of the specificity in motion direction learning.

These results may also provide hints at solving another controversy regarding location specificity of orientation discrimination learning. Like motion direction learning, orientation learning is found to be strictly specific to the trained location in an early study by Shiu and Pashler (1992). However, significant and sometimes complete transfer of orientation learning from one visual quadrant to another is observed more recently by us (Zhang, Xiao, Klein, Levi, & Yu, 2010) and by Hung and Seitz (2014). We notice that Shiu and Pashler also studied orientation discrimination learning with the single-level MCS method, but Zhang, Xiao et al. (2010) and Hung and Seitz (2014) used staircase methods in their trainings. As discussed in Zhang, Xiao et al. (2010), the orientation stimuli in Shiu and Pashler (1992) contained local cues (e.g., edges of a monitor) that could be used by the observers. This potential local cue usage is likely facilitated by single-level MCS training.

The local-cue learning effects apparently are not the whole story of learning specificity. As Figs. 2f and 3a show, motion direction learning is very much direction specific even with jittered or staircase-varied stimuli. So is foveal orientation discrimination learning that shows orientation specificity with staircase training (Zhang, Zhang et al., 2010; Zhang, Xiao et al., 2010). Vernier learning and contrast discrimination learning with staircase training are also location and orientation specific (Wang et al., 2014; Xiao et al., 2008; Yu et al., 2004). However, these specific learning effects may not be explained by extra local-cue learning that is possibly resistant to staircase training. Previously we created a double training method and its variations (e.g., the TPE method) to enable complete transfer of perceptual learning to untrained conditions (Xiao et al., 2008; Zhang, Zhang et al., 2010). Specifically, learning becomes significantly more transferrable if the observers are additionally exposed to the untrained transfer location or feature

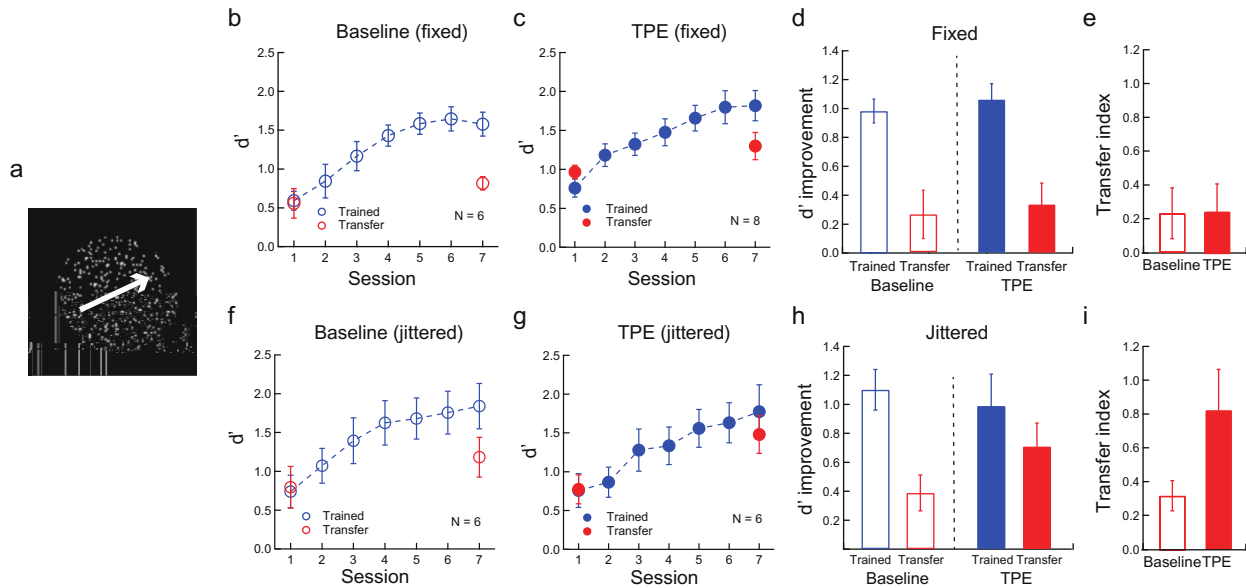


Fig. 2. The effects of TPE training on direction transfer of motion direction learning with fixed and jittered directions. (a) Stimuli. (b) The session-by-session d' data in the baseline condition with fixed directions. (c) The session-by-session d' data in a TPE design with fixed directions. (d) Improvements of d' at trained and transfer directions in baseline and TPE training with fixed directions. (e) The transfer indices in baseline and TPE training with fixed directions. (f) The session-by-session d' data in the baseline condition with jittered directions ($\pm 2^\circ$) while the direction difference remained unchanged. (g) The session-by-session d' data in a TPE design with jittered directions. (h) Improvements of d' at trained and transfer directions in baseline and TPE training with jittered directions. (i) The transfer indices in baseline and TPE training with jittered directions.

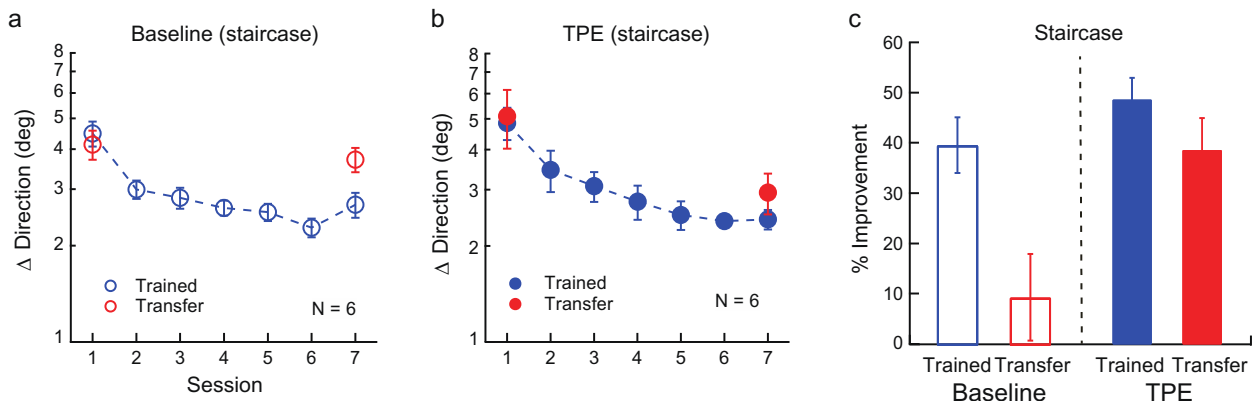


Fig. 3. TPE-enabled transfer of motion direction learning to untrained directions with staircase training. (a) The session-by-session threshold data in the baseline condition. (b) The session-by-session threshold data in a TPE experimental design. (c) A summary of improvements of direction discrimination thresholds in baseline and TPE conditions.

dimension via an irrelevant task. This is even true when a physically distinct stimulus is used in the irrelevant task (Mastropasqua, Galliussi, Pascucci, & Turatto, 2015; Wang, Cong, & Yu, 2013). Although it is likely that the secondary training with the same stimulus (e.g., a Gabor) could reduce local-cue learning in double training, a physically distinct stimulus (e.g., moving dots vs. Gabor) is not expected to introduce the same local-cue learning effects to enable significant and sometime complete transfer. Rather our recent evidence suggests that learning specificity (in staircase trained tasks) is more likely related to a lack of top-down modulation and bottom-up stimulation at untrained conditions, so that learning cannot functionally connect to these untrained conditions to enable learning transfer (Xiong, Zhang, & Yu, 2015; Yu, Xiong, & Zhang, 2015). Apparently in these staircase training cases the TPE method works only when learning is already available for transfer.

Figs. 1 and 2 show that training-induced d' improvements are similar in fixed and jittered direction conditions. In the fixed con-

ditions the observers may primarily learn to use local cues to make the direction judgment. In the jittered conditions when the local cues are disturbed, the observers now have to learn to use real motion cues. In both ways the observers could achieve similar d' gains even they learn to primarily use a different set of cues. It is unclear whether the learning effects will differ for extended training period. Fixed-direction training can keep improving the d' for as long as 3 weeks as shown in Liang et al. (2015a).

Unlike limited learning transfer to the contralateral or diagonal locations, there is a complete learning transfer to the ipsilateral location in the fixed-direction condition. We suspect that the observers may learn to use similar stimulus cues associated with the near-fixation side of the moving-dot pattern for direction judgments in ipsilateral locations. These cues are different at contralateral and diagonal locations if the observers still use the near-fixation side of the moving-dot pattern for direction judgment. That is, “more clockwise” means the near-fixation side of the moving-dot pattern moving down in one side of the visual field,

but up in the other side. This cue difference could potentially explain the observed location specificity at contralateral and diagonal quadrant locations. It could even explain the higher learning transfer to the ipsilateral location than to contralateral and diagonal locations in jittered-direction condition.

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