



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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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 observers' less uncertainty with the fixed stimuli than with the ever-changing stimuli. The brain thus can learn to pay more precise attention to the fixed stimuli. However, such precise attention is disturbed when the stimuli are switched to a new location or direction, which causes learning to be specific to the trained condition to some degree. Another potential local cue may be related to the brain's stronger adaptation to the fixed stimuli than to ever-changing ones. There is evidence that adaptation may be at least partially responsible for the learning specificity (Harris, Glikhsberg, & Sagi, 2012). The adaptation status is changed when the stimuli are switched to a new location or direction, which can also produce location and/or direction specificity. In addition, some irrelevant cues from experimental settings, such as the monitor edge, can also be picked up by the observers. Again the same cues may not be available or useful at a new stimulus location or direction. In contrast, all these local cues are much less a concern in staircase training because they are disturbed by the changing stimuli.

Therefore, we hypothesize that local-cue learning may be at least partly responsible for the discrepancies in the transfer effects of motion direction learning. Specifically, for location specificity, learning of some local cues with the single-level MCS method may not be transferrable to a new retinal location, which may have led to stronger location specificity in Ball and Sekuler (1982, 1987). Meanwhile for direction specificity, single-level MCS training may also lead to learning of local cues that are not transferrable to an untrained direction even with a TPE method. However, with staircase training observers may have to learn the real motion direction task, and this learning, as we suggested earlier, is transferrable to untrained directions with TPE training.

A simple way to test our hypothesis is to disturb the local cues during single-level MCS training even if we do not know exactly what these local cues are. To do so, in the current study we jittered slightly the directions of the stimulus pair that define the direction difference by the same amount while keeping the direction difference unchanged in single-level MCS training. This measure allowed the stimulus directions to vary trial by trial, as in staircase training, to disturb the local cues that the observers could normally use in single-level MCS training. Our results did show that the direction jitter enabled significantly more transfer of motion direction learning to untrained quadrants or hemisphere, and to untrained directions with TPE training. These results thus help explain the discrepancies among various studies regarding location and direction specificity and transfer in motion direction learning.

2. Methods

2.1. Observers and apparatus

Forty-three observers in their early 20s participated in this study. All had normal or corrected-to-normal vision, and were new to visual psychophysical experiments and naive to the research purpose. Informed consent was obtained from each of them before data collection. The study has been carried out in accordance with the Declaration of Helsinki for experiments involving humans.

The stimuli were generated with a Psychtoolbox-3 (Pelli, 1997) and were presented on a 21-inch Sony G520 color monitor. The monitor specifications were 1024 pixel $\times$ 768 pixel resolution, 0.39 mm $\times$ 0.39 mm pixel size, 120 Hz frame rate, and 58.2 cd/m² mean luminance for presenting peripheral motion stimuli; and 1600 pixel $\times$ 1200 pixel resolution, 0.24 mm $\times$ 0.24 mm pixel size, 100 Hz frame rate, and 42.2 cd/m² mean luminance for presenting foveal motion stimuli. The luminance of the monitor was linearized by an 8-bit look-up table. A chin-and-head rest was used to stabilize the head of the observer. Experiments were run in a dimly lit room. An Eyelink 1000 (SR Research, Kanata, Ontario, Canada) was used to monitor eye movements in half the observers in peripheral learning tasks. Trials were excluded from data analysis if eye positions deviated from the fixation point more than 2° before the stimulus onset.

2.2. Stimuli

The peripheral motion stimuli were identical to those used in a previous study (Wang et al., 2014). Each stimulus consisted of 25 black random dots (4 $\times$ 4 pixels each), which was regenerated for every presentation. The stimulus appeared in an invisible (mean luminance) 2°-diameter circular window that was centered in a visual quadrant at 5° retinal eccentricity (Fig. 1a). When a dot reached its lifetime (250 ms) or traveled out of the stimulus window, a new dot emerged from the other side of the window at a random position. All dots moved in the same direction at a speed of 7°/s.



“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.

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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 = $[0.44 \text{ } 1.00]$), including two showing complete learning transfer ($TIs = 0.94 \text{ } 1.00$). 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.

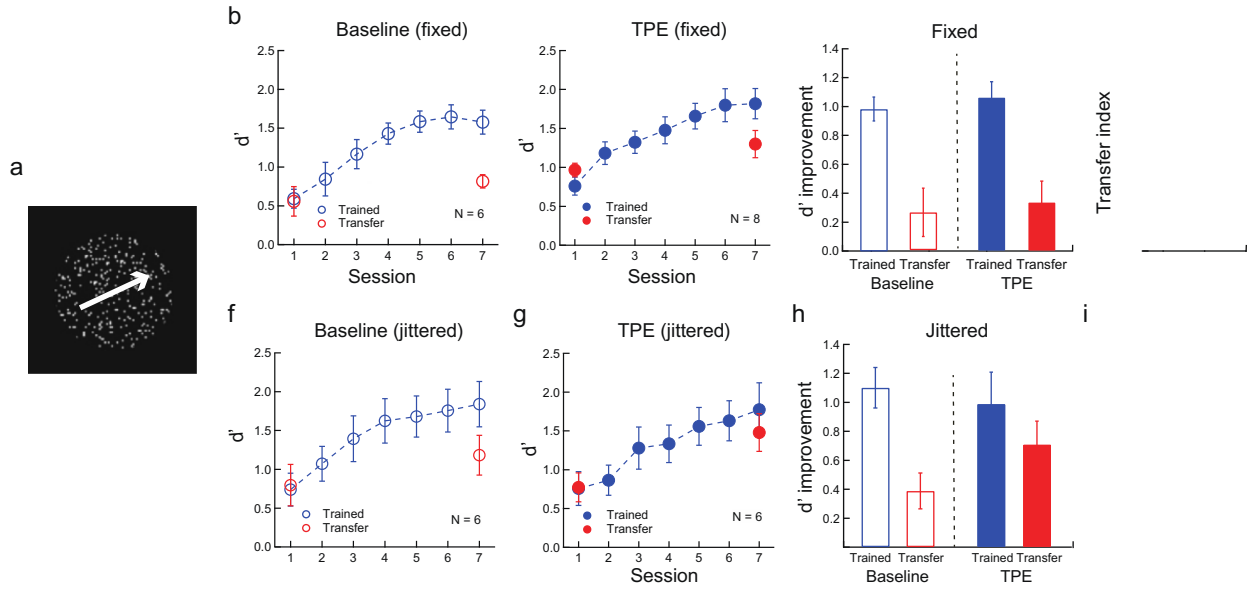
We then performed TPE training with another group of observers, which again involved original motion direction training and additional exposure to the transfer direction via a dot-number discrimination task. Training reduced direction thresholds at the trained direction by $48.4 \pm 4.4\%$ ($p < 0.001$, 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 Pashler direction

The local-cue learning effects apparently are not the whole story of learning specificity. As Figs. 2f and 3a show, motion direction learning is 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



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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