



Perceptual learning of motion direction discrimination transfers to an opposite direction with TPE training



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ABSTRACT

Motion direction learning is known to be specific to the trained direction. However, in this study we used our recently developed TPE (training-plus-exposure) method to demonstrate that motion direction learning can transfer to an opposite direction. Specifically, we first replicated the strict direction specificity of motion direction learning with a group of moving dots. However, when the participants were exposed to the opposite direction in an irrelevant dot number discrimination task, either simultaneously with motion direction training or at a later time, but not in a reversed order, motion direction learning transferred to the opposite direction significantly and sometimes completely. These results suggest that motion direction learning may be a high-level process in which the brain learns the potentially transferable rules of reweighting the motion direction inputs. However, we speculate that high-level learning may not functionally connect to sensory neurons that are tuned to other directions but are not stimulated during training, which leads to direction specificity. It is the stimulus exposure in TPE training that connects high-level learning to the exposed opposite direction to enable learning transfer.

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1. Introduction

Perceptual learning of motion direction discrimination, like learning of many other basic visual features such as contrast, orientation, spatial frequency, and Vernier discrimination (Fiorentini & Berardi, 1980; Schoups, Vogels, & Orban, 1995; Crist et al., 1997; Fahle, 1997; Yu, Klein, & Levi, 2004), has been reported to be specific to the trained retinal location and feature at least under near-threshold conditions (Ball & Sekuler, 1982, 1987; Liu, 1999; Liu & Weinshall, 2000; Shibata et al., 2012). For example, Ball and Sekuler (1982, 1987) reported that training improves the direction discrimination of moving dots, but the learning cannot transfer to an untrained opposite direction, or to an untrained retinal location/hemifield. These and similar specificities in other visual learning tasks have led to the assumptions that visual perceptual learning may occur in early visual areas that are retinotopic and selective to basic visual features (Ball & Sekuler, 1982, 1987; Karni & Sagi, 1991; Schoups, Vogels, & Orban, 1995; Crist et al., 1997; Bejjanki et al., 2011).

Alternatively, as Mollon and Danilova (1996) pointed out, learning specificities do not necessarily imply plasticity in early visual areas. Perceptual learning could be central and high level, but specific to what the brain learns. Indeed, Liu and Weinshall (2000) dis-

covered that although motion direction learning is specific to the trained direction, ensued learning of a new direction becomes faster, suggesting that motion direction learning involves some high-level processes. Moreover, based on their findings that monkey motion direction learning is associated with response changes in decision-related LIP neurons, not the middle temporal area neurons that are known to decode motion signals (Law & Gold, 2008), Law and Gold (2009) proposed a reweighting model in which the decision areas learn to readout the motion inputs from a specific population of MT neurons that respond to the motion stimuli. Because MT is retinotopic and MT neurons are direction selective, this model is able to account for the direction and location specificities in motion direction learning.

However, even the very concept of perceptual learning being location and feature specific is being challenged. In recent studies we developed new training methods that enable location and orientation specific perceptual learning, such as contrast, orientation, Vernier, feature detection, and texture discrimination learning to transfer to untrained retinal locations (Xiao et al., 2008; Wang et al., 2012; Wang, Cong, & Yu, 2013) and orientations completely (Zhang et al., 2010). Directly relevant to the current study, Zhang et al. (2010) used a TPE (training-plus-exposure) method to enable foveal orientation discrimination learning to transfer to an orthogonal orientation. Specifically, the participants were first trained with one orientation, and learning showed no transfer to an orthogonal orientation. However, if the participants were also exposed to the orthogonal orientation through an irrelevant contrast

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discrimination task, either simultaneously with training (in alternating staircases) or at a later time, learning transferred completely to the orthogonal orientation. These transfer effects suggest that the brain is not simply learning how to readout or reweight the specific orientation inputs activated by the stimuli, but more general rules of reweighting orientation inputs. These rules are applicable to other untrained orientations.

Previous studies from our lab have been limited to tasks that can be categorized as form vision. In the current study we extended our investigation to the motion perception domain, with particular interests in testing whether a TPE training procedure could abolish the direction specificity of motion direction learning and enable learning transfer. The outcomes of this study would provide new insights into the neural mechanisms underlying motion learning, as well as the existing psychophysical, neurophysiological and brain imaging data on motion perceptual learning.

2. Methods

2.1. Participants and apparatus

Data were collected from 17 participants (undergraduate students in their early 20s). All had normal or corrected-to-normal vision, and were naïve to psychophysical testing and the purposes of the study. They received brief practice of motion direction discrimination (one staircase) at the trained direction before data collection. Informed written consent was obtained from each participant before data collection.

The stimuli were generated with a Psychtoolbox-3 (Pelli, 1997) and presented on a 21-inch Sony G520 color monitor (1600 pixel \times 1200 pixel resolution, 0.24 mm \times 0.24 mm pixel size, and 75 Hz frame rate). The mean luminance of the monitor was 50 cd/m². The luminance of the monitor was linearized by an 8-bit look-up table. A chin-and-head rest helped stabilize the head of the participant. Experiments were run in a dimly lit room. Viewing was binocular for foveal testing.

2.2. Stimuli

The foveal motion stimulus consisted of 400 white random dots (3 \times 3 pixels each at the maximal luminance) in an invisible 8°-diameter black (minimal luminance) circular window centered on a black monitor screen. All dots moved in the same direction (22.5° or 202.5°) at a speed of 10°/s. Each dot had a lifetime of 400 ms minus a random starting time of 0–400 ms. When a dot reached its lifetime, a new dot was generated at a random position within the stimulus window following the same lifetime rule. When a dot traveled out of the stimulus window, a new dot entered from the other side of the window at a random position, again following the same lifetime rule. The viewing distance was 0.8 m.

2.3. Procedure

Direction discrimination and dot-number discrimination thresholds were measured with a temporal 2AFC staircase procedure. In each trial the reference and test (reference direction \pm Δ direction or reference dot-number \pm Δ dot-number) were separately presented in two 500 ms stimulus intervals in a random order separated by a 200 ms inter-stimulus interval. A small green fixation point preceded each trial by 300 ms and stayed through the trial. In the motion direction discrimination task, the participants judged which interval the random dots moved in a more clockwise direction. In the dot-number discrimination task, the

participants judged which interval contained more dots. Auditory feedback was given on incorrect responses.

Thresholds were estimated using a classical 3-down-1-up staircase rule that resulted in a 79.4% convergence level. Each staircase consisted of four preliminary reversals and six experimental reversals (approximately 50 trials). The step size of the staircase was 0.05 log units. The geometric mean of the experimental reversals was taken as the threshold for each staircase run. Each pre- and post-training threshold was averaged on the basis of 5 staircases (approximately 250 trials). Each training session consisted of 20 staircases and lasted about 1.5 h. Only one training session was conducted on a single day.

3. Results

3.1. Experiment I. Direction-specific motion learning transfers to an opposite direction with TPE training

We first replicated direction specificity in a foveal motion direction discrimination task (Fig. 1). Six participants practiced direction discrimination at 22.5° or 202.5° (Δ Dir_dir1, read as “direction discrimination at direction 1”). Significant learning was evident after five sessions of training (Mean Percent Improvement (MPI) = 40.0 \pm 5.5%, $t = 7.21$, $df = 5$, $p < 0.001$; One-tailed paired t -test was used here and in later data analyses; Fig. 1b and c), but training had no significant impact on direction discrimination at an opposite direction (Δ Dir_dir2, $t = 1.06$, $df = 5$, MPI = 5.7 \pm 5.4%, $p = 0.17$), showing very strong direction specificity of motion direction learning.

To test whether TPE training could abolish direction specificity from motion direction learning, the same six participants were then exposed to an opposite direction while discriminating the number of the dots moving in this opposite direction (Δ Num_dir2, the actual direction was jittered $\pm 10^\circ$ around the opposite direction trial by trial). The purpose of having the participants perform demanding near-threshold dot-number discrimination was to divert attention away from the stimulus direction. After four sessions of dot-number discrimination training (MPI = 19.5 \pm 6.4%, $t = 3.03$, $df = 5$, $p < 0.015$; Fig. 1b and c), direction discrimination for the untrained opposite direction (Δ Dir_dir2) was significantly improved (MPI = 20.3 \pm 5.6%, $t = 3.60$, $df = 5$, $p = 0.008$) with all six participants' data averaged. Here two participants actually did not show the transfer effects. They might be regarded as outliers since another six participants in the next simultaneous TPE experiment all showed significant transfer (Fig. 2). In Experiment III we will show that dot-number discrimination training alone had no significant impact on motion direction threshold (Fig. 3). The overall MPI of Δ Dir_dir2 after the TPE procedure was 24.6 \pm 7.3% ($t = 3.38$, $df = 5$, $p = 0.010$), about two thirds of the 40.0% improvement due to direct training, suggesting that a majority of the motion direction learning now transferred to an opposite direction after TPE training.

A transfer index (TI), defined as $MPI_{\text{untrained}}/MPI_{\text{trained}}$, was used to compare the transfer of learning among different training conditions. TI = 1 indicated complete transfer, and TI = 0 indicated no transfer. For the above TPE procedure, TI was 0.17 after the initial training phase, and increased to 0.62 after the subsequent exposure phase.

3.2. Experiment II. The effects of simultaneous TPE training on the transfer of motion direction learning

In Experiment I the training phase preceded the exposure phase in a successive TPE training design, so that performance at the opposite direction was pre-tested twice, once before the training

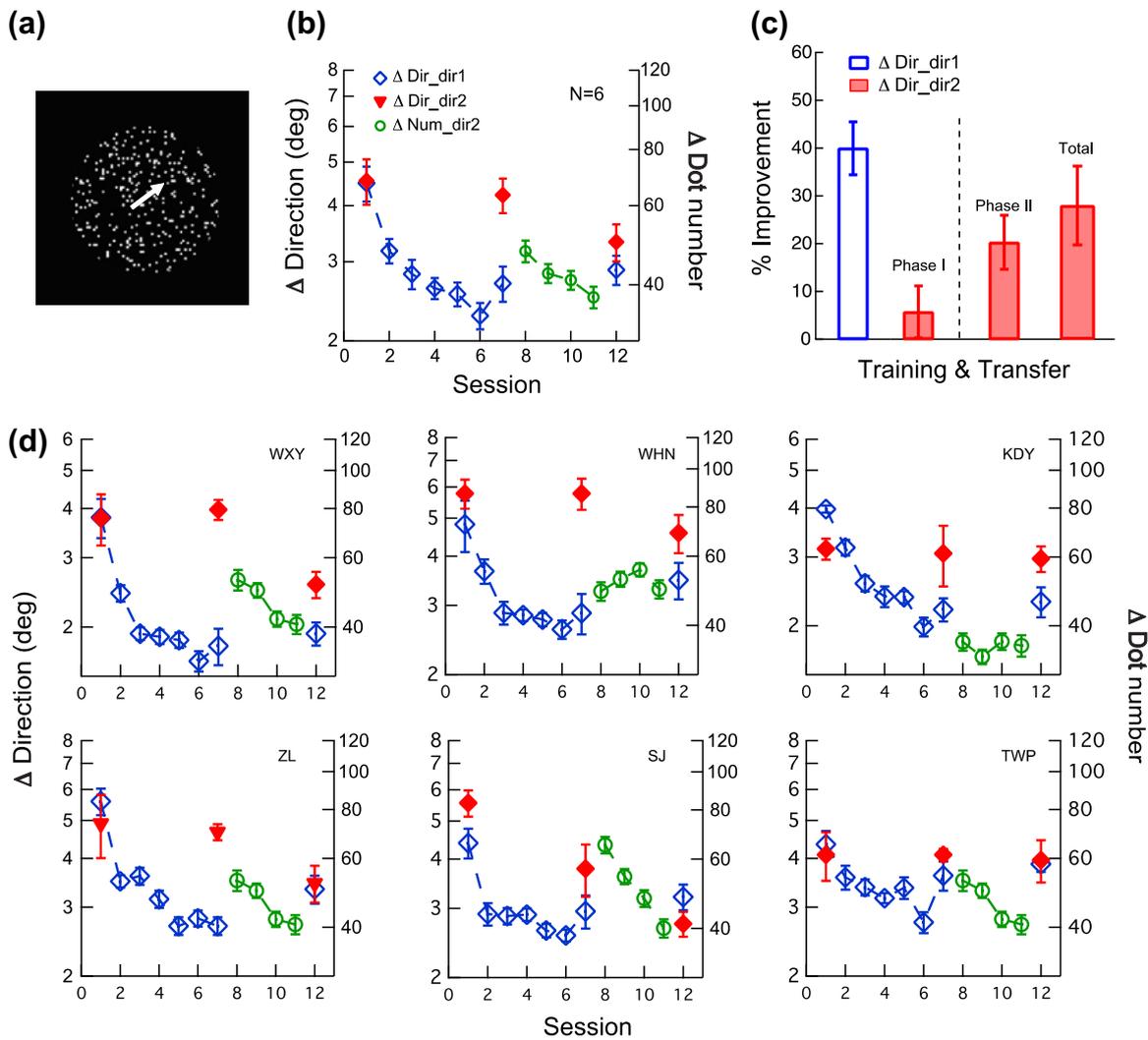


Fig. 1. Direction-specific motion learning transfers to an opposite direction with TPE training. (a) Stimuli for foveal motion direction discrimination. (b) Baseline and TPE training: Direction discrimination was first practiced at one direction (22.5° or 202.5°, $\Delta\text{Dir}_{\text{dir}1}$, direction thresholds indicated by the left ordinate) and the transfer of learning was tested at an untrained opposite direction (202.5° or 22.5°, $\Delta\text{Dir}_{\text{dir}2}$), which showed typical direction specificity. A dot-number discrimination task with dots moving in the transfer direction ($\Delta\text{Num}_{\text{dir}2}$, dot-number thresholds indicated by the right ordinate) was then practiced for transfer direction exposure. Thresholds were averaged over all participants' data, and error bars represented one standard error of the mean. The left and right ordinates have the same scale factor in log units. (c) A summary of performance improvement due to learning and transfer: Left bars – Learning and transfer after the training phase; middle bar – transfer after the exposure phase; right bar – overall transfer. (d) Individual data.

phase and once before the exposure phase, which could confound the estimation of the amount of learning transfer. To reduce this confounding effect, six new participants completed a simultaneous TPE procedure in which they practiced $\Delta\text{Dir}_{\text{dir}1}$ and $\Delta\text{Num}_{\text{dir}2}$ simultaneously in alternating blocks of trials (staircases; 10 staircases for each task per session). All other experimental conditions were identical to those in Experiment I. This simultaneous procedure significantly improved motion direction discrimination at the trained direction ($\Delta\text{Dir}_{\text{dir}1}$; $\text{MPI} = 28.0 \pm 4.1\%$, $t = 6.76$, $df = 5$, $p < 0.001$; Fig. 2a, b), as well as at an untrained opposite direction in all participants ($\Delta\text{Dir}_{\text{dir}2}$; $\text{MPI} = 26.9 \pm 3.9\%$, $t = 6.88$, $df = 5$, $p < 0.001$) by a similar amount ($t = 0.16$, $df = 5$, $p = 0.44$). The transfer index TI was 1.2, indicating complete transfer of motion direction learning. Together the successive and simultaneous TPE training results demonstrate that motion direction learning could transfer to an opposite direction quite significantly and sometimes completely.

In addition, we tested the learning transfer to other neither trained nor exposed directions that were 45°, 90°, and 135° from the trained direction, respectively (Fig. 2a and b). Learning trans-

ferred much less to these directions ($\text{MPI} = 11.5 \pm 5.2\%$, $t = 2.19$, $df = 5$, $p = 0.040$, $\text{TI} = 0.47$, pooled over three directions). Previously we found that after TPE training orientation learning also transferred much less to orientations that are away from either the trained or the exposed orientations (Zhang et al., 2010). Why learning transfers less to these neither trained nor exposed orientations or directions after TPE training will be discussed later in the context of our proposal that orientation and motion direction learning is a rule-based high-level process.

3.3. Experiment III. The effects of reversed-order TPE training on learning transfer

In the above experiments, the exposure task (dot-number discrimination) was trained either after or simultaneously with the motion direction task. In this new experiment we reversed the order of TPE training, i.e., the exposure task was trained before motion direction training, for two purposes. First, the transfer of initial dot-number discrimination learning to motion direction discrimination at the same direction served as a baseline for previous

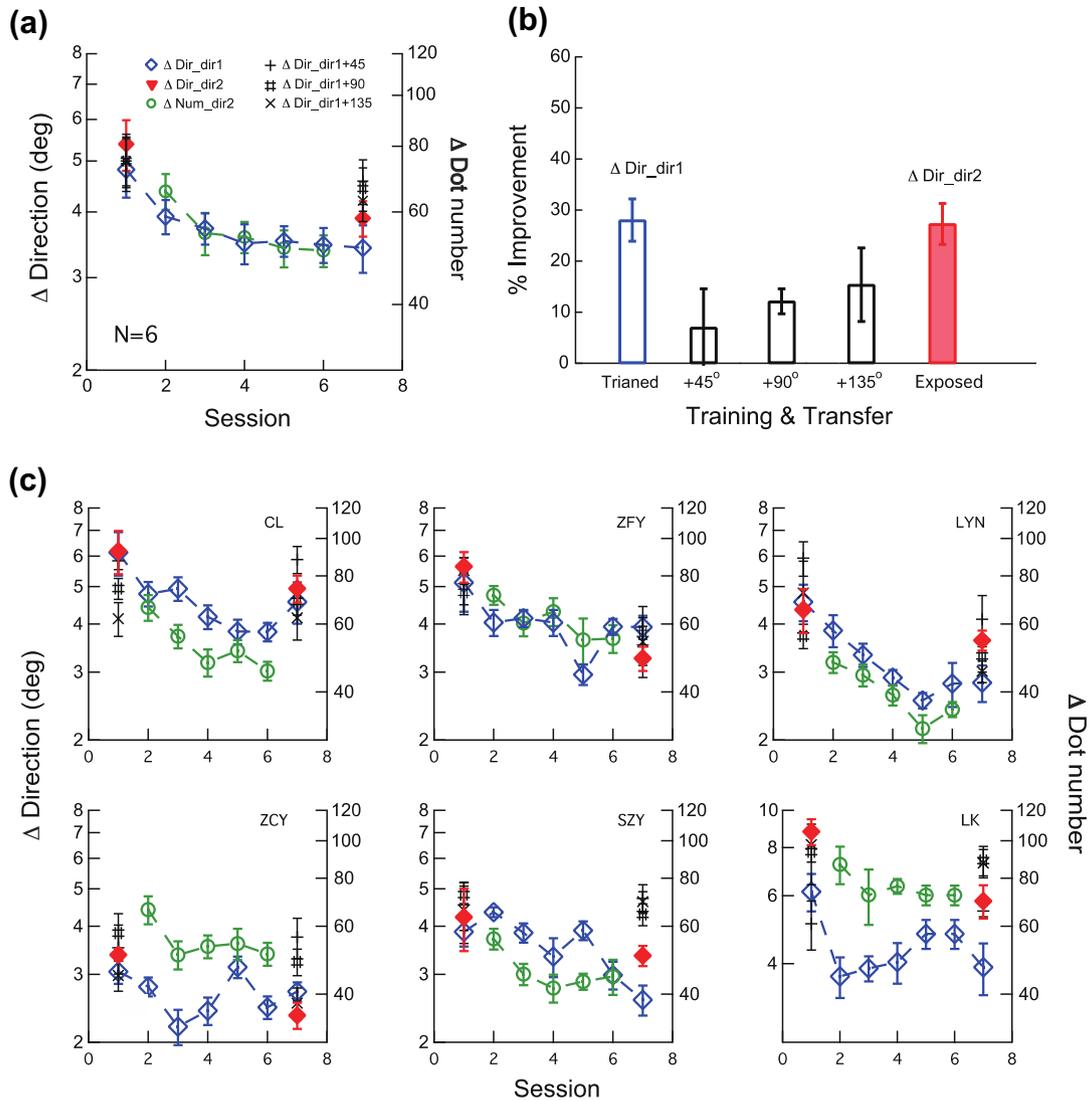


Fig. 2. Transfer of motion direction learning with simultaneous TPE training. (a) Simultaneous TPE training: Direction discrimination training (ΔDir_dir1) as well as dot-number discrimination training (ΔNum_dir2) for transfer direction exposure were conducted simultaneously in separate staircases. Learning transfers to the exposed opposite direction (ΔDir_dir2), as well as to three other neither trained nor exposed directions that were 45° , 90° , and 135° from the trained direction, were tested. (b) A summary of performance improvement due to learning and transfer. (c) Individual data.

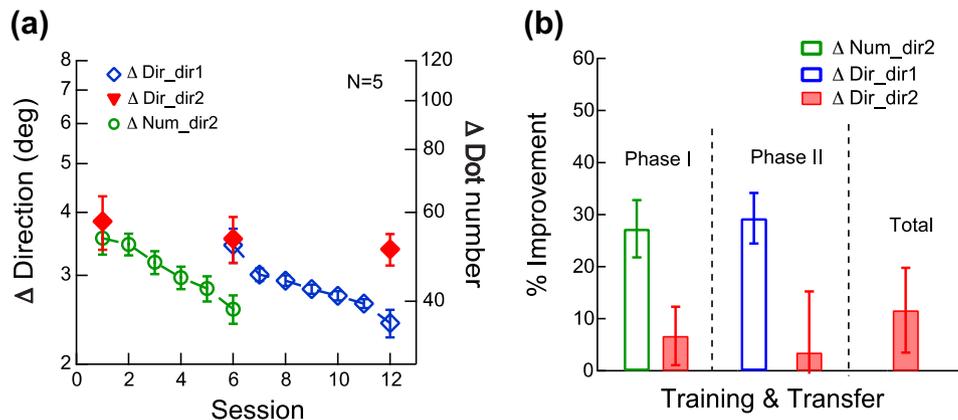


Fig. 3. Transfer of motion direction learning with reversed-order TPE training. (a) The dot-number discrimination training (the exposure task) at the opposite direction preceded the motion direction training. (b) A summary of performance improvement due to learning and transfer.

TPE-enabled learning transfer. That is, whether the mere exposure of the opposite direction through dot-number discrimina-

ing was sufficient to improve motion direction discrimination at the same direction? Fig. 3 shows that the dot-number discrimina-

tion training ($\Delta\text{Num_dir2}$; $\text{MPI} = 27.3 \pm 5.5\%$, $t = 4.94$, $df = 4$, $p = 0.004$) had no significant impact on the motion direction thresholds ($\Delta\text{Dir_dir2}$; $\text{MPI} = 6.7 \pm 5.6\%$, $t = 1.20$, $df = 4$, $p = 0.15$), indicating that the TPE enabled motion direction learning transfer (Figs. 1 and 2) did not result from the mere exposure of the opposite direction, but from the entire TPE procedure.

The second purpose of this experiment was to replicate an interesting finding with TPE-enabled orientation learning transfer in motion learning tasks. That is, once the TPE order was reversed, the learning transfer to an orthogonal orientation disappeared (Zhang et al., 2010). Fig. 3 shows that in the second phase of the reversed-order TPE training, although training improved motion direction discrimination at a trained direction ($\Delta\text{Dir_dir1}$; $\text{MPI} = 29.3 \pm 4.8\%$, $t = 6.04$, $df = 4$, $p = 0.002$), learning failed to transfer to an opposite direction ($\Delta\text{Dir_dir2}$; $\text{MPI} = 3.5 \pm 11.7\%$, $t = 0.30$, $df = 4$, $p = 0.39$). Therefore the transfer of motion direction learning also disappeared with a reversed-order TPE procedure. The implications of this reversed-order TPE training in understanding the mechanisms underlying motion direction and orientation learning will be discussed later.

4. Discussion

Our results demonstrate that, like orientation learning that can be rendered completely transferrable to an orthogonal orientation with TPE training (Zhang et al., 2010), motion direction learning can become significantly and sometimes completely transferable to an opposite direction with similar TPE procedures. These transfer results suggest that motion direction learning is a high-level learning process.

The neurophysiological study by Law and Gold (2008) is most relevant to our results. They discovered that motion direction learning in monkeys is a high-level process, in that the performance improvements are not correlated to the response changes of direction-selective MT neurons, but to those of LIP neurons that are related to decision making. In a later reweighting model (Law & Gold, 2009), they suggested that motion direction learning results from improved readout of the initial noisy responses of MT neurons responding to the motion stimulus by a high-level decision unit. Our results could improve this high-level reweighting model in a significant way: After learning the decision unit apparently can deal with motion inputs from MT neurons representing other directions with similar and sometimes equal precision. This is a case-based general learning process in which the decision unit learns the general rules of reweighting motion inputs regardless of their specific directions.

As we pointed out earlier, existing psychophysical studies on motion direction learning also hint at the involvement of high-level processes. Liu (1999) reported that the direction specificity in motion direction learning depends on the task difficulty. Learning is transferrable to other untrained directions if the task is easy and suprathreshold. Moreover, even for hard near-threshold learning that shows strong direction specificity, later learning becomes faster when the participants continue to practice at a new direction (Liu & Weinsall, 2000). These results indicate that high-level processes play important roles in motion direction learning. Our results go one step further by showing that even the direction specificity under the near-threshold or “hard” learning conditions can be completely abolished through TPE training. This finding indicates that motion direction learning is mainly a high-level process, since an even partially low-level learning process would not explain complete learning transfer.

Why is motion direction learning specific to the trained direction in the first place with conventional training, and why does it transfer much less to other unexposed directions after TPE train-

ing? The same questions apply to orientation learning with similar results (Zhang et al., 2010). The transfer results indicate that the brain learns the rules of performing a specific task such as motion direction or orientation discrimination that are potentially transferrable. However, these rules may not apply to other untrained directions or orientations because high-level learning may not be able to functionally connect to neurons that are tuned to these directions or orientations but are not stimulated during training. It is the exposure to a new direction or orientation in TPE training that stimulates relevant direction or orientation neurons to promote the connections from high-level learning to allow learning transfer. This account is consistent with the reversed-order TPE training results with the transfer of motion direction learning (Fig. 3) and orientation learning (Zhang et al., 2010). These results suggest that the only possible role of direction or orientation exposure is to activate and connect untrained direction or orientation to high-level learning that either has been or is being developed (Treue & Martinez Trujillo, 1999; Martinez-Trujillo & Treue, 2004).

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