Bottom-up and top-down factors of motion direction learning transfer

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Abstract

Perceptual learning of motion discrimination has long been believed to be motion direction specific. However, recent studies using a double-training paradigm, in which the to-be-transferred condition was experienced through practicing an irrelevant task, found that perceptual learning in various visual tasks, including motion direction discrimination, can transfer completely to new conditions. This transfer occurred when the transfer stimulus was subconsciously presented, or when top-down attention was allocated to the transfer stimulus (which was absent). In the current study, observers were exposed subconsciously, or directed top-down attention, to the transfer motion direction, either simultaneously or successively with training. Data showed that motion direction learning transferred to the transfer direction, and suggest that motion direction learning specificity may result from under-activations of untrained visual neurons due to insufficient bottom-up stimulation and/or lack of top-down attention during training. These results shed new light on the neural

mechanisms underlying motion perceptual learning and provide a constraint for models of motion perceptual learning.

Keywords: perceptual learning; motion direction; specificity; learning transfer; double training

Introduction

Visual perceptual learning refers to improvement in perceptual performance as a result of training or experience. It takes place in various visual tasks involving basic visual features, such as contrast, orientation, and motion information (see Fahle & Poggio, 2002; Gilbert, Sigman, & Crist, 2001, for reviews). One hallmark of perceptual learning is that it is typically specific to the trained locations and features (e.g., orientation) (Ahissar & Hochstein, 1997; Ball & Sekuler, 1987; Fahle, 1994; Karni & Sagi, 1991). This is often taken as an evidence that V1 neurons are responsible for a large degree of specificity (Fiorentini & Berardi, 1981; Karni & Sagi, 1991; Schoups, Vogels, & Orban, 1995; Schoups, Vogels, Qian, & Orban, 2001) because neurons in V1 are most retinotopic (Tootell, Silverman, Switkes, & De Valois, 1982) and orientation selective (Hubel & Wiesel, 1959). This hypothesis has also been supported by neurophysiological studies which found that training could sharpen neuronal orientation tuning in the primary visual cortex (Schoups et al., 2001; Teich & Qian, 2003). However, Ghose, Yang, and Maunsell (2002) did not find any orientation tuning changes in either V1 or V2 neurons. Petrov, Dosher, and Lu (2005) further suggested that modification of early cortical representations might not be necessary for orientation discrimination learning. Instead, the read-out connections to a decision unit were proposed to be reweighted through training. Following these pioneering studies, during the past decade, many procedures have been developed to show that learning can indeed transfer from trained to untrained conditions (see Herzog et al., 2017, for a review), suggesting that perceptual learning may occur in higher stages of visual processing than the sensory cortices. Among these procedures, the "double-training" or "training-plus-exposure" procedures (Xiao et al., 2008; Zhang et al., 2010) are two of the most widely used. With a "double-training" procedure, Xiao et al. (2008) employed a contrast training procedure at one location, and task-irrelevant location training at a different location. The results showed that the additional location training enabled a complete learning transfer across locations. In another study, Zhang et al. (2010) adopted a training-plus-exposure (TPE) procedure, in which observers were trained at one orientation and passively exposed to a second orientation. It was found that learning of orientation perception transferred completely from the training orientation to the exposure orientation (i.e., the transfer orientation). A rule-based learning model was proposed, stating that perceptual learning is most likely a high-level rule-based learning process and thus potentially transferrable to untrained conditions (Zhang et al., 2010). By default, the learned rules do not apply to the untrained conditions automatically because the functional connectivity between the low-level neurons (responding to the untrained conditions) and the high-level areas is usually unestablished, leaving the learning specific to the trained conditions. However, if the untrained locations and features have been activated (e.g., via a double training or TPE procedure), the learning rules will be applied to these untrained locations and features due to the newly established functional connectivity between the low visual cortices and the high-level areas, leading to a transfer of learning to the untrained conditions (Xiao et al., 2008; Zhang et al., 2010).

Furthermore, in a more recent double-training study, Xiong, Zhang, & Yu et al. (2016) isolated the influence of bottom-up stimulation and top-down attention on learning transfer with a continuous flash suppression (CFS) method (Tsuchiya & Koch, 2005). Participants were trained on a task (e.g., Vernier discrimination) at one location, and were exposed to the same stimulus sub-consciously at another location (the bottom-up stimulation condition), or were asked to attend to another location where no stimulus was presented (the top-down condition). It was shown that both the bottom-up stimulation and top-down attention manipulations independently enabled significant learning transfer, supporting the rule-based learning model (e.g., Zhang et al., 2010).

Although Xiong, Zhang et al. (2016) questioned learning specificity that had dominated perceptual learning research for decades, and offered new insight into the rule-based learning models, some critical questions were not answered. First of all, the Vernier discrimination and orientation discrimination tasks are arguably a type of visual form processing. It remains unknown whether bottom-up stimulation and top-down attention could also facilitate transfer of motion perceptual learning. Secondly, previous studies have demonstrated that perceptual skills might consolidate off-line during overnight sleep (see Peigneux & Smith, 2010, for a review). Thus the functional connection mentioned in Xiong, Zhang et al.'s study (2016) may established before consolidation because training and the bottom-up stimulation/top-down attention manipulations were administered across blocks on the same day. It is therefore unclear whether functional connection can also be established after learning have already been consolidated.

To address the concerns mentioned above, the current study adopted the paradigm used by Xiong, Zhang et al. (2016) to investigate the effect of bottom-up stimulation and top-down attention on motion discrimination learning transfer. In the bottom-up stimulation (of the untrained motion direction) condition, motion discrimination was trained in one direction, with stimuli in the transfer direction being rendered invisible with CFS (Tsuchiya & Koch, 2005). In the top-down attention (to the untrained motion direction) condition, participants were asked to voluntarily attend to the transfer direction while there was, in fact, no stimulus presented. To address the second issue, bottom-up stimulation and top-down attention were separately applied either at the same time of training (the training and the bottom-up/top-down manipulations in alternative blocks in the same session) or after training (the bottom-up/top-down manipulations applied after five sessions of training). If the same learning rule as found in previous studies (e.g., Xiong, Zhang, et al., 2016) also governs motion learning, we would expect a significant transfer of motion learning in these two conditions mentioned above. Furthermore, if transfer-facilitation effect of the bottom-up stimulation and top-down attention could still be effective after learning has already been consolidated, the learning transfer should be observed to be at the same magnitude no matter whether the manipulation was applied simultaneously or sequentially.

Materials and method

Observers and apparatus

Thirty-one naïve volunteers from Peking University (aged 21.7 ± 2.4 years; 16 male and 15 female) and eighteen from Soochow University (aged 22.2 ± 2.0 years; 6 male and 12 female) participated in the current study. There were at least six observers in each experiment (see Table 1 for details). Five out of the six observers in each of Experiments 1, 2A, 2B, 2C, and 3B were recruited from Peking University; the remaining observers in these experiments were recruited from Soochow University. All 6 observers in Experiment 3A were recruited from Peking University, and all observers in Experiments 4 and 5 were recruited from Soochow University. All observers had normal or corrected-to-normal vision (measured with a Tumbling E chart), gave written informed consent. The study was approved by the academic and ethics committees of Peking University and Soochow University, in agreement with the Declaration of Helsinki.

Both in Peking University and Soochow University, Dell Optiplex 9020 equipped with an NVIDIA Quadro FX 4600 graphics card were used. Stimuli were presented on 21-inch Dell P1230 CRT monitors (1600 × 1200 resolution, 0.25 × 0.25 mm per pixel, 85-Hz refresh rate). The mean luminance (average of minimal and maximum luminance, measured with a ColorCal MKII photometer, Cambridge Research Systems Ltd., Cambridge, UK) of the monitor was 41.5 cd/m^2 at Peking University and 41.1 cd/m^2 at Soochow University (for more details about the monitors, see Zhang et al., 2018). The luminance was linearized by an 8-bit look-up table. Stimuli were prepared with MATLAB (MathWorks, Inc., Natick, MA, USA) and Psychtoolbox-3 (Brainard, 1997; Pelli, 1997). Experiments were run in dimly lit rooms, with a chin-and-head rest stabilizing the heads of the observers.

Experiments

Five experiments were conducted in this study and are summarized in Table 1. All experiments measured the participants' motion direction discrimination thresholds before (Session 1) and after training (Session 7 and Session 13), with five training sessions between the measurements of thresholds (Sessions 2-6 and Sessions 8-12). The training sessions took place across several days, with each training session completed within a single day, and the next training session coming up one or two days afterward. Before each experiment, there was a block of practice trials with a staircase procedure (about 50 trials), showing motion stimuli in both the to-be-trained direction and the transfer direction. Experiment 1 measured the motion direction learning specificity and recorded the baseline training performance. Experiment 2A measured the effect of the bottom-up stimulation on learning transfer. Experiment 2B was designed to exclude the alternative account that the bottom-up stimulation alone can induce motion learning in the transfer direction. A further Experiment 2C was included to exclude the possibility that transfer can be caused by noise stimulation instead of the bottom-up stimulation in the transfer motion direction.

Table 1. Experiments and tasks in the current study. In each experiment, motion direction discrimination thresholds were measured pre-training and post-training, with five training sessions in between. Various training designs were used across experiments. In Experiments 1-3B, there was only one training phase (Phase I), where the bottom-up/top-down manipulations were applied simultaneously with the main training when applicable. In the last two experiments, the bottom-up/top-down manipulations were applied subsequently in Phase II.

		Phase I			Phase II	
	Sample size	**Session 1**	**Sessions 2-6 (training)**	**Session 7**	**Sessions 8-12 (training)**	**Session 13**
Exp 1: Training baseline	6	Threshold	Motion discrimination	Threshold		
Exp 2A: Simultaneous bottom-up	6	Threshold	Motion discrimination & color discrimination	Threshold		
Exp 2B: Bottom-up only	6	Threshold	Color discrimination	Threshold		
Exp 2C: Simultaneous noise	6	Threshold	Motion discrimination & color discrimination	Threshold		
Exp 3A: Simultaneous top-down	6	Threshold	Motion discrimination & motion detection	Threshold		
Exp 3B: Top-down only	6	Threshold	Motion detection	Threshold		
Exp 4: Subsequent bottom-up	6	Threshold	Motion discrimination	Threshold	Color discrimination	Threshold
Exp 5: Subsequent top-down	7	Threshold	Motion discrimination	Threshold	Motion detection	Threshold

Moving on from the bottom-up contribution to the top-down factor, Experiment 3A measured the effect of top-down attention on learning transfer. Experiment 3B was designed to exclude the possibility that top-down attention alone can induce motion learning in the transfer direction. Experiments 4 and 5 were utilized to explore whether the transfer-facilitation effect of the bottom-up stimulation and top-down attention could still be effective after learning have already been consolidated. To achieve this purpose, Experiments 4 and 5 were carried out in two phases: motion direction training was completed in Phase I; the bottom-up stimulation or top-down attention manipulation was subsequently applied in Phase II, which was separated from Phase I by 1-2 days. In these last two experiments, the post-training thresholds were measured twice in Sessions 7 and 13.

In all the experiments, for both the training and transfer motion directions, there were at least 5 blocks of stimuli in Sessions 1, 7, and 13. If the variation was too large (i.e., the standard error of the mean threshold values across blocks was larger than 10% of the averaged threshold), we would consider the learning still unstable, and another block of trials would be added immediately for both the trained and transfer motion directions at the end of the session. Thus, each threshold in Sessions 1, 7, and 13 was averaged on the basis of 5-6 staircases. The arithmetic mean across measurements for each condition was used as the discrimination threshold (both pre-training and post-training). In Sessions 2-6 and Sessions 8-12, each task listed in Table 1 was repeated for 10 blocks. For motion discrimination, there were around 50 trials (with a staircase procedure) in each block. For color discrimination and motion detection, each block had 50 trials. In Sessions 2-6 of

Experiments 2A, 2C, and 3A, the two different tasks were switched every five blocks, with the motion discrimination task always being conducted first.

Stimuli

Different stimuli were independently presented in the central vision of two eyes using a stereoscope, with motion stimuli in the non-dominant eye and white-noise patterns in the dominant eye. The motion stimulus consisted of 356 random white dots (0.05° in diameter, about 83 cd/m^2) in an imaginative circular window with a diameter of 6° over a gray (about 41 cd/m^2) background at the center of the screen. All dots moved in the same direction (36° or 126° in polar coordinates) at a speed of 6°/s. Each dot had a lifetime of 100 ms minus a random starting delay of 0-100 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, the dot would disappear, and a new dot would enter from the other side of the window at a random position, again following the same lifetime rule.

To separate the potential bottom-up and top-down contributions, the CFS technique (Tsuchiya & Koch, 2005) was applied in the training phases. The CFS configuration consisted of a square flashing white-noise pattern (8.70° × 8.70°) in the central vision of the dominant eye. The white-noise pattern, refreshed at 9.4 Hz for 953 ms, consisted of randomly generated ovals of random sizes (the minor axis of the smallest ellipse was 0.08°, and the major axis of the largest ellipse was 0.33°) and random luminance (from 0 to about

83 cd/m^2). In the bottom-up stimulation condition, the motion stimuli, which moved orthogonally to the trained motion direction, was presented in the non-dominant eye in half of the trials (Figure 1). As the signal of the motion stimuli was much weaker than the flashing noise patterns, the observers should not be able to detect the motion stimuli. To confirm this suppression effect of CFS, eight observers (3 from Experiment 2A, 2 from Experiment 2B, and 3 from Experiment 4) were tested with a two-alternative forced choice (2AFC) motion detection task in which either a motion stimulus at the transfer direction or a blank screen was presented to the non-dominant eye, with the flashing noise pattern presented to the dominant eye (60 trials per block for 3 blocks). The observers were asked to determine whether there was a motion stimulus. The result showed chance-level performance (0.49 ± 0.01), suggesting a full suppression effect of the CFS used in the current study. Therefore, we concluded that the results of learning transfer in Experiments 2A and 4 were not contaminated by the leakage of the motion perception. Furthermore, to prevent the observers from perceiving the abrupt presentation of the motion stimuli, the luminance of the motion stimuli increased gradually from the mean luminance (about 41 cd/m^2) to the maximal luminance (57.9 cd/m^2) and then back to the mean luminance following a Gaussian function in time. In the top-down attention condition, only a white fixation was displayed in the non-dominant eye.

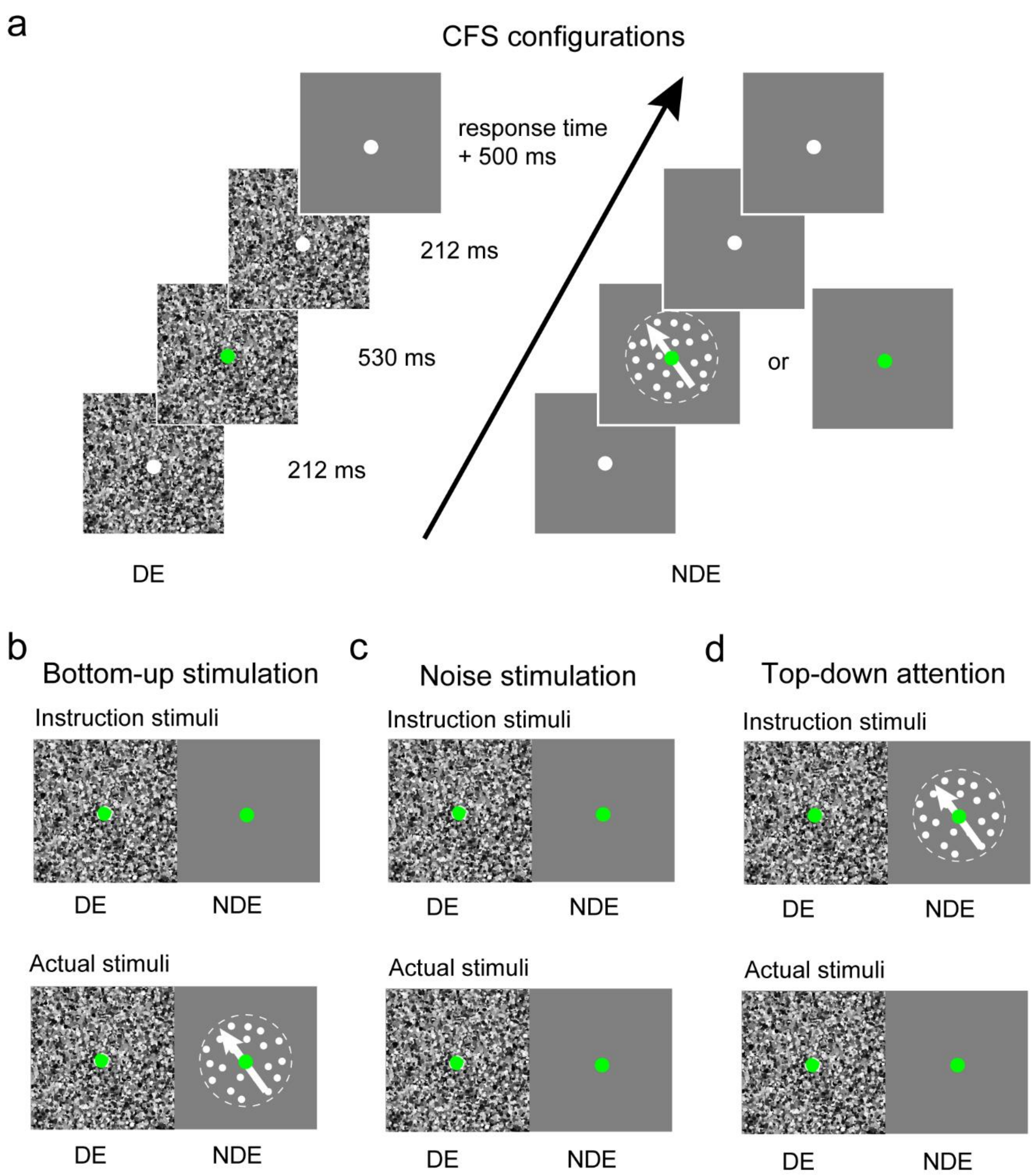

Figure 1. Stimuli used in the current study. (a) Schematic diagram of continuous flashing suppression (CFS) configurations, which were used in the bottom-up stimulation (actual stimuli) and also in the top-down attention instruction. The flashing white-noise pattern was presented for 953 ms in the dominant eye. At 213 ms after pattern onset, a motion stimulus in the transfer motion direction was presented in the non-dominant eye for 530 ms in half of the trials and was absent in the other half of the trials. The fixations in both eyes turned

green or red at the same time when the motion stimulus (or a blank screen) was presented. (b) Stimuli for the bottom-up stimulation manipulation. Bottom-up stimulation was achieved subconsciously with the bottom-up stimuli presented in the non-dominant eye but not mentioned in the instructions. (c) Stimuli in the noise stimulation condition. The motion stimuli were not presented or mentioned in the instructions. (d) Stimuli for the top-down attention manipulation. The top-down attention was achieved by requesting the participants to discriminate the motion direction in the non-dominant eye (instruction stimuli), despite that the motion stimulus was in fact not presented in the test (actual stimuli). DE: dominant eye; NDE: non-dominant eye.

Tasks and procedures

Three tasks were used in the current study: a motion direction discrimination task, a color discrimination task, and a motion detection task. In the motion direction discrimination task, motion direction discrimination thresholds were measured with a temporal 2AFC, 3-down-1-up staircase procedure (with a convergence level of 79.4%). In each trial, the reference and test stimuli (reference direction ± Δdirection) were sequentially presented for 506 ms in a random order with a 506-ms inter-stimulus interval in between. A small white fixation point (0.25° in diameter) preceded each trial by 506 ms and remained on the screen throughout the trial. The observers were asked to determine which of the two stimuli contained a motion more clockwise in its direction. A brief auditory feedback was given on incorrect responses. Each staircase consisted of four preliminary reversals and six experimental reversals (approximately 50 trials in total) and started with an initial motion direction difference of 11.2°. This value was about twice the average threshold revealed in previous studies using identical stimuli (Xiong, Xie, & Yu, 2016), thus easily discriminable. The step size of the staircase was 0.05 log-units. The geometric mean of the six experimental reversals was taken as the threshold for each staircase.

The color discrimination task was used to examine the effect of the bottom-up stimulation and noise stimulation manipulations on the motion direction learning transfer. In both of the bottom-up stimulation and noise stimulation conditions, the color of the fixation dot (in both eyes) randomly changed to green or red for 530 ms from 212 ms after the onset of the 953-ms CFS noise pattern (see Figure 1a). The observers were asked to discriminate the color of this fixation color change (instruction stimuli shown in Figure 1b). No feedback was provided. In the bottom-up stimulation condition, the stimulus in the non-dominant eye was either only a fixation dot or a motion stimulus moving orthogonally to the trained motion directions (also with a fixation dot; Figure 1b). In the noise stimulation condition, the motion stimulus was never displayed (Figure 1c).

After having completed the testing, eighteen of the observers who participated in the bottom-up stimulation condition were asked whether they saw a motion stimulus while performing the color discrimination task. Only two observers reported having noticed a motion stimulus occasionally but reported wrong motion directions, showing very limited awareness of the motion stimuli. Because the observers did not notice the existence of the motion stimuli, the motion stimuli stimulated the visual cortex at the transfer motion direction without being consciously perceived.

The motion detection task was used to engage top-down attention to the transfer motion direction and check its effect on learning transfer. In this task, the color of the fixation dot was always white, with a blank screen always displayed to the non-dominant eye (actual stimuli in Figure 1d). To convince the observers that the motion stimuli were present in half of the trials, in the first practice trial, a motion stimulus in the direction orthogonal to the training direction was shown in the non-dominant eye with maximal luminance (instruction stimuli in Figure 1d). The luminance decreased over trials until observers reported that they could not detect the motion stimulus anymore. The observers were told that the nearly undetectable stimulus towards the end of the practice would be used in the experiment. The observers were then asked to report, or to guess if they had to, whether a motion stimulus was shown by making a key press. Fake feedback with a random accuracy score between 55% and 70% was provided by the end of each block. This paradigm ensured the top-down attention being directed to the transfer motion direction without any bottom-up stimulation.

Results

Experiment 1: Baseline performance − Motion direction learning specificity

Six subjects took part in this experiment, and training significantly reduced the threshold by 42.5 ± 4.5% (mean ± SE, mean percent improvement = [threshold $_{\text{pre-training}}$ – threshold $_{\text{post-training}}$]/ threshold $_{\text{pre-training}}$) in the trained motion direction (t_5 = 9.37, p < .001, 95% CI = 30.8% to 54.1%, one-sample *t*-tests against 0 in in this and later analyses if not specified; Cohen's *d* = 3.82; Figure 2). It is worth noting that *t*-test may not be an appropriate method for ratio data analysis because ratio data may not be normally distributed. Therefore, to provide additional converging evidence, a Wilcoxon signed-rank test was also performed, and a consistent statistical result was found (p = .028). Training reduced the motion direction discrimination threshold in the (untrained) orthogonal direction only by 14.0 ± 3.3% (t_5 = 4.19, p = .009, 95% CI = 5.4% to 22.5%; p = .028 with a Wilcoxon signed-rank test; Cohen's *d* = 1.71). The improvement was significantly weaker in the transfer motion direction than in the trained motion direction (t_5 = 11.62, p < .001, 95% CI = 22.2% to 34.8%; p = .028 with a Wilcoxon signed-rank test; Cohen's *d* = 4.75), indicating that the learning only transferred partially from the trained to the transfer direction. This shows the motion-direction learning specificity.

A transfer index (TI) was calculated to compare the transfer effects between motion directions. TI was defined as the improvement at the transfer condition divided by the improvement at the trained condition, with TI = 0 indicating a complete learning specificity (no transfer at all), and TI = 1 indicating a complete learning transfer. If a TI value was more than 3 SDs away from the group average, it was considered an outlier and was replaced by the theoretical maximum or minimum, which was 1 or 0 respectively. The usage of the minimum or the maximum depended on whether the TI value was more than 3 SDs above or below the group average. According to this criterion, only one participant in Experiment 4 exhibited an outlier TI value (TI = 2.83). In the baseline condition, TI = 0.31 ± 0.06, which was significantly larger than 0 (t_5 = 5.43, p = .003, 95% CI = .16 to .45; p = .028 with a Wilcoxon test; Cohen's d = 2.22). This significant performance improvement in the untrained orthogonal direction may be due to some unspecific factors irrelevant to the motion perception (e.g., procedure learning).

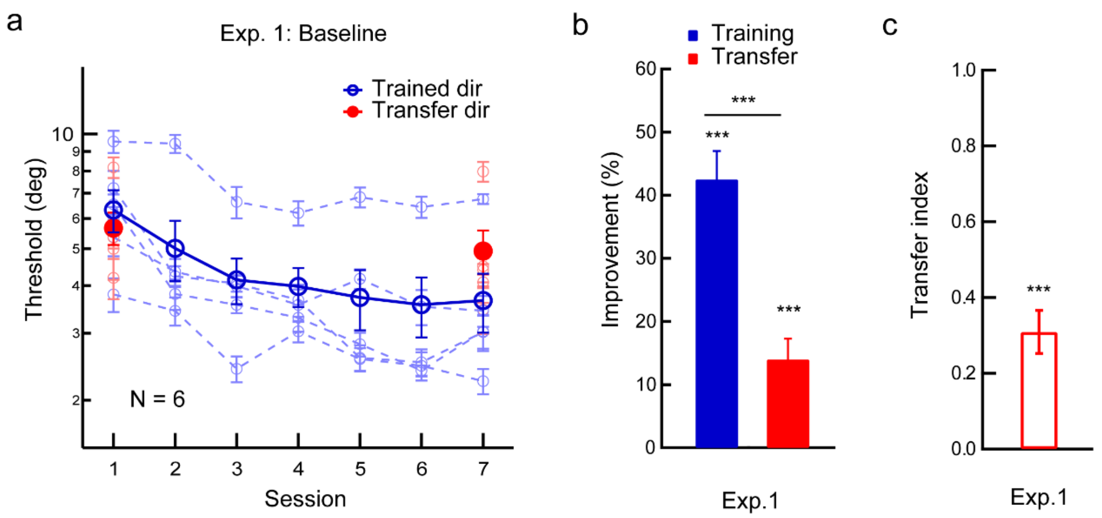

Figure 2. Results of Experiment 1, showing the baseline performance of the motion direction learning. (a) The mean and individual learning and transfer data. Individual data are plotted (dash lines) together with the averaged results (solid line). (b) Performance improvements in the trained and transfer motion directions. (c) Transfer index in the baseline condition. Error bars indicate ±1 standard errors of the means. *** $p < .001$.

Experiment 2: Learning transfer - Effect of bottom-up stimulation

Zhang and Yang (2014) demonstrated that motion discrimination learning could completely transfer to an untrained direction orthogonal to the trained direction if the observers received exposure to the transfer motion direction in a motion-irrelevant secondary task. In the current study, the observers received the motion direction training and the bottom-up stimulation in the transfer motion direction in separate blocks of the same sessions (Experiment 2A). The results are summarized in Figure 3. Five sessions of training reduced the motion discrimination threshold in the trained motion direction significantly by 39.6 ± 3.7% (t_5 = 10.63, p < .001, 95% CI = 30.1% to 49.2%; p = .028 with a Wilcoxon test; Cohen's d = 4.34), as well as in the untrained but bottom-up stimulated orthogonal motion direction by 32.5 ± 2.4% (t_5 = 13.30, p < .001, 95% CI = 26.2% to 38.8%; p = .028 with a Wilcoxon test; Cohen's d = 5.43) (Figures 3a and 3d). Transfer was substantial but not complete, as suggested by a significant difference between the improvements in the two directions (t_5 = 4.77, p = .005, 95% CI = 3.3% to 11.0%; p = .028 with a Wilcoxon test; Cohen's d = 1.95), leading to a TI of 0.83 ± 0.03 (Figure 3e).

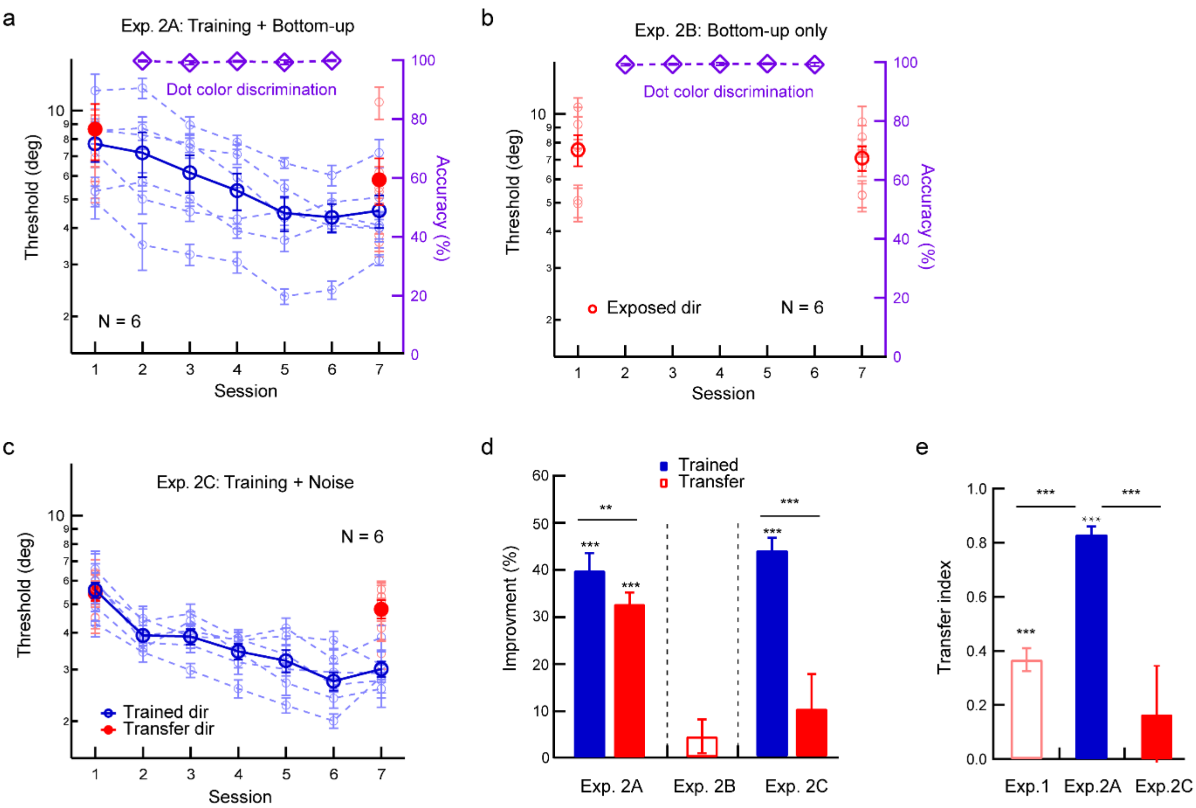

Figure 3. Results of Experiment 2, illustrating the performance during motion direction learning and the effect of the simultaneous bottom-up stimulation in the transfer motion direction. (a) The mean (solid line) and individual (dash lines) learning and transfer data with the bottom-up stimulation in the transfer motion direction (Experiment 2A). (b) Results of the control experiment (Experiment 2B), which applied the bottom-up stimulation but not the motion direction training. (c) Results of another control experiment (Experiment 2C), which employed the motion direction training and the white-noise stimulation but not the bottom-up stimulation. (d) A summary of learning and transfer performance in training plus bottom-up stimulation, bottom-up stimulation alone, and training plus noise-only conditions. (e) A summary of the transfer indices in the baseline (replotted from Figure 2c), training plus bottom-up stimulation, and training plus noise-only conditions. Error bars indicate ±1 standard errors of the means. ** $p < .01$; *** $p < .001$.

The first control experiment (Experiment 2B) indicated that the bottom-up stimulation alone could not account for the performance improvement in the untrained orthogonal motion direction. In this experiment, six new observers received an equal amount of bottom-up stimulation in the orthogonal transfer motion direction without receiving training with the motion discrimination task. The bottom-up stimulation did not significantly decrease the motion direction discrimination threshold in the stimulated motion direction (improved by 4.4 ± 3.6%, $t_5 = 1.24$, $p = .27$, 95% CI = -4.7% to 13.6%; $p = .25$ with a Wilcoxon test; Cohen's $d = .51$, Figures 3b and 3d).

The second control experiment (Experiment 2C) ruled out the possibility that the dynamic white noise, which could have activated visual neurons that were tuned to all motion directions, was sufficient to cause the same amount of learning transfer. The experimental design was the same as that of Experiment 2A, except that no orthogonal motion stimulus was present in the actual stimuli. Again, training reduced motion direction discrimination threshold significantly by 44.0 ± 3.0% (t_5 = 14.52, p < .001, 95% CI = 36.2% to 51.8%; p = .028 with a Wilcoxon test; Cohen's d = 5.93) (Figures 3c and 3d). However, learning transfer was not significant in the transfer motion direction (10.0 ± 7.8%, t_5 = 1.28, p = .26, 95% CI = -10.1% to 30.1%; p = .25 with a Wilcoxon test; Cohen's d = .52). This transfer measure was also significantly lower than the improvement in the trained motion direction (t_5 = 6.59, p = .001, 95% CI = 20.7% to 47.3%; p = .028 with a Wilcoxon test; Cohen's d = 2.69). The TI was 0.17 ± 0.18 in this condition (Figure 3e).

A Kruskal-Wallis test revealed significant differences among the TIs in the baseline condition (Figure 2a), the training plus bottom-up stimulation condition (Figure 3a), and the training plus noise-only condition (Figure 3c) (p = .003). Post-hoc Dunn's multiple comparisons indicated that the training plus bottom-up stimulation condition had significantly more transfer than the baseline condition (p = .015, corrected in this and later Post-hoc Dunn's multiple comparisons) and the training plus noise-only condition (p = .007). There was no significant difference between the TIs of the baseline and the training-plus-noise-only conditions (p = 1.00).

These results collectively suggest that the bottom-up stimulation in the transfer motion direction enabled significantly more transfer of motion direction learning than in the baseline condition (Experiment 1), although transfer was incomplete. These results are consistent with Zhang et al.'s study (2014), which suggested that motion direction learning is likely to be a high-level process and could transfer to another direction as a result of functional connectivity between high-level brain areas and sensory neurons tuned to the transfer motion direction. Moreover, results in the current experiment further suggested that the functional connectivity can be achieved via exposure to subliminal motion stimuli.

Experiment 3: Learning transfer - Effect of top-down attention

Top-down attention is often necessary for obtaining training-related performance improvement (Ahissar & Hochstein, 1993; Fahle, 1997, 2004). For example, when there were two Vernier stimuli, discrimination accuracy only improved for the attended stimulus but not the unattended stimulus (Fahle, 2004). In Experiment 3, we examined the effect of the top-down attention on the learning transfer instead of the learning itself. Specifically, we investigated whether learning in one motion direction, with the help of the top-down attention to another motion direction (training plus top-down attention), would transfer to the transfer motion direction. The results are summarized in Figure 4. Training and the top-down attention to the transfer motion direction reduced motion direction threshold in the trained motion direction by 39.3 ± 3.2% (t_5 = 12.13, p < .001, 95% CI = 31.0% to 47.6%; p = .028 with a Wilcoxon test; Cohen's d = 4.95, Experiment 3A) (Figures 4a and 4c). The threshold reduction in the direction orthogonal to the training direction was also significant (30.2 ± 3.8%, $t_5 = 8.04$, $p < .001$, 95% CI = 20.5% to 39.9%; $p = .028$ with a Wilcoxon test; Cohen's $d = 3.28$), suggesting a learning transfer. Analysis based on null-hypothesis significance test found that the improvement in the untrained motion direction was not statistically different from that in the trained motion direction ($t_5 = 1.77$, $p = .137$, 95% CI = -4.1% to 22.3%, Cohen's $d = .72$), with a TI value of 0.80 ± 0.14. This suggests a possibility that the learning transfer was complete. However, a further Bayesian *t*-test found no evidence for the hypothesis that there was any difference between the improvements in the trained and untrained motion directions, $BF_{10} = 1.02$ (Marsman & Wagenmakers, 2017), with a Cauchy prior width of 0.707 in this (and also later) Bayesian *t*-tests.

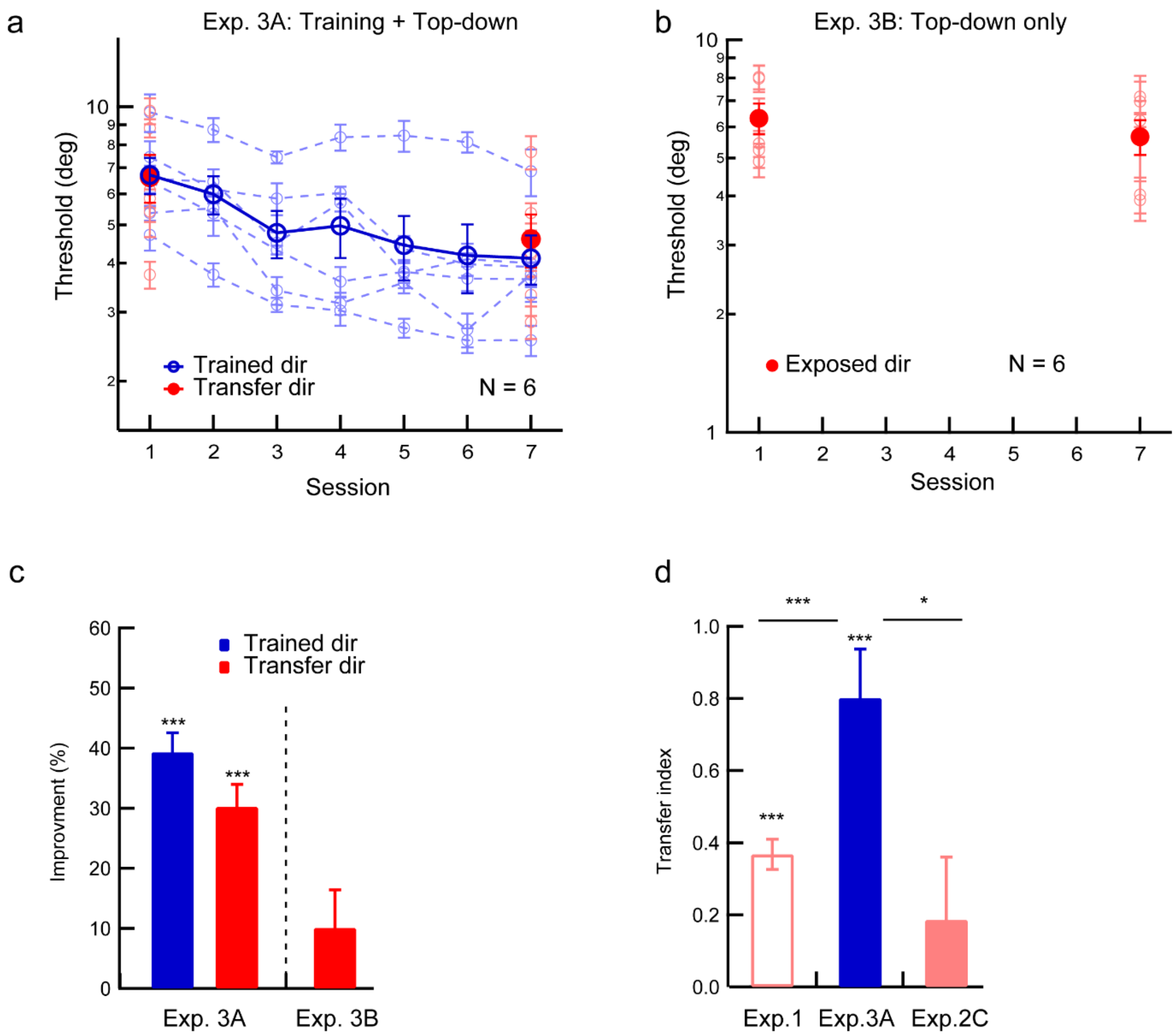

Figure 4. Results of Experiment 3, demonstrating the motion direction learning and the effect of simultaneous top-down attention to the transfer motion direction. (a) The mean (solid line) and individual (dash lines) learning and transfer data with training and the top-down attention to the transfer motion direction (Experiment 3A). (b) Results of the control experiment (Experiment 3B) without the motion discrimination training. (c) A summary of the learning and transfer effects in the top-down attention and control experiments. (d) A summary of the transfer indices in the training plus top-down attention condition, the previous baseline condition (replotted from Figure 2c), and the training plus noise-only condition (replotted from Figure 3e). Error bars indicate ±1 standard errors of the means. * *p*

< .05; *** $p < .001$.

The control experiment (Experiment 3B) with six observers demonstrated that, without actual training of motion direction discrimination, top-down attention to the transfer motion direction alone could not lead to a significant learning effect in the transfer motion direction (10.0 ± 6.3%, $t_5 = 1.59$, $p = .17$, 95% CI = -6.2% to 26.4%; $p = .17$ with a Wilcoxon test; Cohen's $d = .65$) (Figures 4b and 4c).

A Kruskal-Wallis test revealed significant differences among the TIs in the baseline condition (Figure 2a), the training plus top-down attention condition (Figure 4a), and the training plus noise-only condition (Figure 3c) ($p = .008$). Post-hoc Dunn's multiple comparisons indicated that the training plus top-down attention condition had significantly more transfer than the baseline condition ($p = .024$) and the training plus noise-only condition ($p = .021$). The difference between the latter two conditions, however, did not reach significance ($p = 1.00$).

These results jointly suggested that the top-down attention to the transfer motion direction enabled significantly more transfer of the motion direction learning than transfer in the baseline condition (Experiment 1). These results are consistent with the rule-based learning model (Zhang et al., 2010), the notion that motion direction learning may be a high-level process. The current finding further suggests that solely attending to the anticipated motion signal (without any physical motion signal stimulating the visual cortex) could functionally link the high-level perceptual learning and low-level neurons which turn to the transfer direction.

Experiment 4: Learning transfer - Effect of subsequent bottom-up stimulation

To explore whether the transfer-facilitation effect of the bottom-up stimulation and top-down attention procedures on training could still be effective after learning have been consolidated, we examined learning transfer by applying the motion discrimination training and the bottom-up stimulation sequentially instead of in the same day.

The results are illustrated in Figure 5. Six new observers received training in the training motion direction, and showed a significant training effect (44.6 ± 3.9%, $t_5 = 11.3$, $p < .001$, 95% CI = 34.5% to 54.8%; $p = .028$ with a Wilcoxon test; Cohen's $d = 4.62$) (Figures 5a and 5b). Before the bottom-up stimulation, the learning significantly transferred to the transfer motion direction (21.4 ± 2.6%, $t_5 = 8.2$, $p < .001$, 95% CI = 14.7% to 28.1%; $p = .028$ with a Wilcoxon test; Cohen's $d = 3.33$), but significantly less than in the training in the trained motion direction ($t_5 = 6.24$, $p = .002$, 95% CI = 13.7% to 32.8%; $p = .028$ with a Wilcoxon test; Cohen's $d = 2.55$). This performance improvement in the transfer motion direction may be caused by procedure learning and learning during the pre-test. After the following bottom-up stimulation, the motion discrimination performance improved further by 19.7 ± 3.2% ($t_5 = 6.20$, $p = .002$, 95% CI = 11.6% to 27.9%; $p = .028$ with a Wilcoxon test; Cohen's $d = 2.53$) in the transfer motion direction. The overall improvement of the transfer motion direction discrimination after training and subconscious bottom-up stimulation was 36.9 ± 3.2% ($t_5 = 11.5$, $p < .001$, 95% CI = 28.7% to 45.2%; $p = .028$ with a Wilcoxon test; Cohen's $d = 4.70$) which was not different ($t_5 = .78$, $p = .47$, 95% CI = -9.0%

to 16.8%, Cohen's d = .32) from the training effect in the trained motion direction (40.9 ± 7.5%, t_5 = 5.45, p = .003, 95% CI = 21.6% to 60.0%; p = .028 with a Wilcoxon test; Cohen's d = 2.22). Although the learning transferred largely to the transfer motion direction, the Bayesian t-test showed no evidence for either supporting or rejecting the hypothesis that the improvement differed between the trained and transfer motion directions (BF_{10} = .48).

The TI was 0.90 ± 0.08 (Figure 5c), which was not statistically different (t_{10} = .75, p = .47, 95% CI = -.26 to .13, Cohen's d = .44) from that in the simultaneous bottom-up stimulation condition (Experiment 2) (TI = 0.83 ± 0.03, the blue bar in Figure 3e). However, a further Bayesian t-test did not show enough evidence for the two TIs being either the same or different (BF_{10} = .56). The high level of learning transfer in the subsequent bottom-up stimulation condition again suggests that the motion learning was more likely a high-level process. More importantly, the result in this experiment demonstrates that the bottom-up stimulation could also enable learning transfer after motion learning have been consolidated.

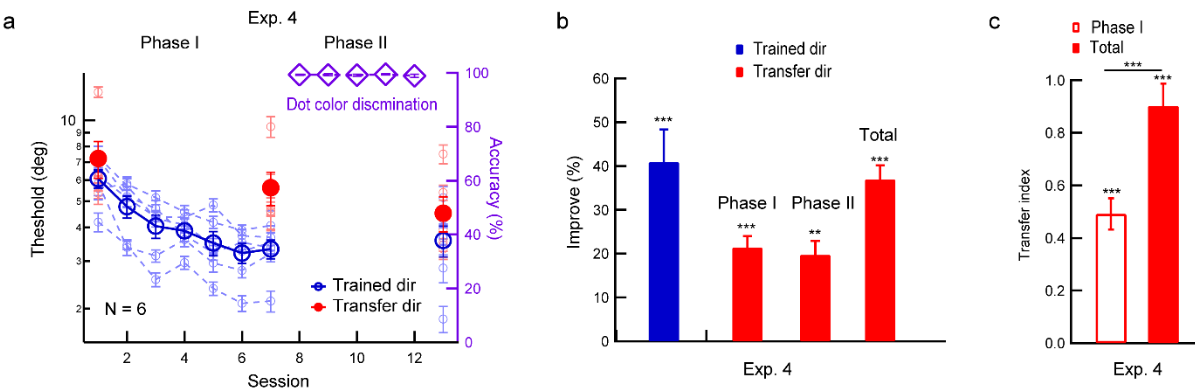

Figure 5. Results of Experiment 4, showing the motion perceptual learning and the effect of subsequent bottom-up stimulation in the transfer motion direction. (a) The mean (solid line) and individual (dash lines) learning and transfer data with training and the subsequent

top-down attention to the transfer motion direction. (b) A summary of the learning and transfer effects. (c) A summary of the transfer indices. Error bars indicate ±1 standard errors of the means. DE: dominant eye. ** $p < .01$; *** $p < .001$.

Experiment 5: Learning transfer - Effect of subsequent top-down attention

We also examined whether the sequential application of the motion discrimination training and the top-down attention (to the transfer motion direction) could lead to a learning transfer to the transfer motion direction. The results are demonstrated in Figure 6. The observers were trained with the motion direction discrimination task for 5 sessions, and showed a significant improvement (51.5 ± 2.6%, $t_6 = 18.8$, $p < .001$, 95% CI = 44.8% to 58.2%; $p = .018$ with a Wilcoxon test; Cohen's $d = 7.11$) in the trained motion direction. A significant improvement in the untrained motion direction was also found (16.6 ± 4.6%, $t_6 = 3.60$, $p = .011$, 95% CI = 5.3% to 27.9%; $p = .018$ with a Wilcoxon test; Cohen's $d = 1.36$), but significantly less than that in the trained motion direction ($t_6 = 9.38$, $p < .001$, 95% CI = 25.8% to 43.9%; $p = .018$ with a Wilcoxon test; Cohen's $d = 3.55$). The transfer motion direction was subsequently attended to in a motion detection task. This led to a further performance improvement of 19.8% ± 2.9% ($t_6 = 6.50$, $p = .001$, 95% CI = 12.4% to 27.3%; $p = .018$ with a Wilcoxon test; Cohen's $d = 2.46$). The overall improvement in the transfer motion direction after training and the top-down attention sessions was 33.9 ± 1.9% ($t_6 = 16.5$, $p < .001$, 95% CI = 28.9% to 38.8%; $p = .018$ with a Wilcoxon test; Cohen's $d = 6.25$), significantly less ($t_6 = 5.16$, $p = .002$, 95% CI = 6.9% to 19.3%; $p = .018$ with a Wilcoxon test; Cohen's $d = 1.95$) than that in the trained motion direction (46.9 ± 3.4%, $t_6 = 13.9$, p

< .001, 95% CI = 38.7% to 55.2%; p = .018 with a Wilcoxon test; Cohen's d = 5.27), indicating a substantial but incomplete learning transfer.

The TI was 0.73 ± 0.04 (Figure 6c), which was not different (t_{11} = .53, p = .61, 95% CI = -.22 to .36, Cohen's d = .29) from that in the simultaneous top-down attention condition (TI = 0.80 ± 0.14, the blue bar in Figure 4d). However, a further Bayesian t-test did not show enough evidence for the two TIs being either the same or different (BF_{10} = .50). These results convergingly suggest that the top-down attention manipulation could also enable learning transfer after motion learning have been consolidated.

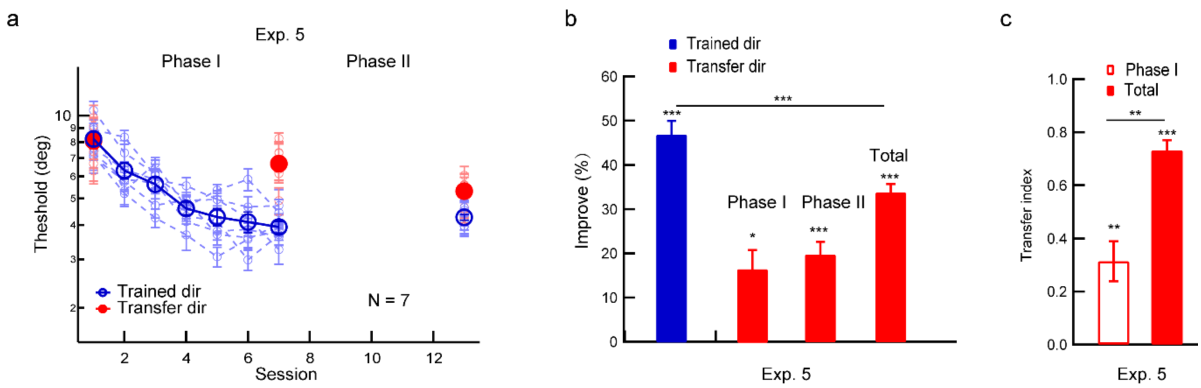

Figure 6. Results of Experiment 5 about the learning and transfer effects of the motion direction discrimination training and the subsequent top-down attention to the transfer motion direction. (a) The mean (solid line) and individual (dash lines) learning and transfer data with training and subsequent top-down attention to the transfer motion direction. (b) A summary of the learning and transfer effects. (c) A summary of the transfer indices. Error bars indicate ±1 standard errors of the means. DE: dominant eye. * p < .05; ** p < .01; *** p < .001.

Discussion

It has been previously found that bottom-up stimulation and top-down attention facilitated learning transfer of form perception (Xiong, Zhang, et al., 2016). The current study extended our understanding by showing that transfer of motion perception could also occur following the bottom-up stimulation and top-down attention manipulations. More importantly, learning transfer observed in the current study suggested that bottom-up stimulation and top-down attention could still be effective after learning have already been consolidated, because the transfer effect was significant even when training and the bottom-up stimulation/top-down attention were conducted sequentially across days. These results offered new insight into the rule-based model (Zhang et al., 2010) by suggesting that functional connectivity between the high level areas and low-level areas which response to transfer motion direction could be established after learning have already been consolidated.

The current results are consistent with Xiong, Zhang et al.'s (2016) study in that learning can transfer to untrained conditions when training is accompanied by passive bottom-up stimulation of the transfer conditions. However, the results are at odds with previous studies by Mastropasqua et al. (2015) and Wang et al. (2012), who reported that passive stimulation in the transfer condition was insufficient to elicit a learning transfer. The most likely explanation for this discrepancy is that the CFS used in the current study and Xiong, Zhang et al.'s (2016) study rendered the passively exposed stimuli subconscious. This could potentially make the stimuli escape suppression from the attention system, or at least make the involvement of the attention system greatly reduced. In contrast, the passively exposed stimuli (as in Mastropasqua et al., 2015) were above the detection threshold, thus could be actively inhibited by attention (Watanabe, Nanez, & Sasaki, 2001). Unfortunately, this explanation fails to explain why only limited learning transfer was found in a more recent study (Lange & De Weerd, 2018) wherein the untrained location was also unconsciously exposed. A careful comparison showed that there are at least two crucial differences between Lange and De Weerd's (2018) study and Xiong, Zhang et al.'s (2016) study. Firstly, Lange and De Weerd used more training sessions (15 sessions) than Xiong, Zhang et al. (6 sessions). Previous studies (Jeter, Dosher, Liu, & Lu, 2010) demonstrated that learning specificity could be enhanced by extensive training. Therefore, the differential transfer effects between these two studies may be accounted for by different amounts of training. Secondly, these two studies quantified learning transfer in different ways. Lange and De Weerd (2018) considered significant improvement in the transfer condition after post-test as an index of specificity, whereas Xiong, Zhang et al. (2016) used the relative improvement between the transfer condition and the trained condition as an index of specificity. The discrepancy in their choices of the definition of specificity (and accordingly the analysis methods) may have also contributed to the diverging conclusions.

Perceptual learning may even occur when people were trained (or were only required to imagine) to discriminate between identical stimuli (Amitay, Irwin, & Moore, 2006; Grzeczkowski, Tartaglia, Mast, & Herzog, 2015). However, the visual learning transfer was limited if there was not enough variance in the feature of the stimuli (e.g., motion direction), even if the double-training paradigm was used (Liang, Zhou, Fahle, & Liu, 2015a). Observers might use some subtle local cues (e.g., edges of a monitor) during training with limited variance in the stimuli (Zhang, Xiao, Klein, Levi, & Yu, 2010). When a feature of the stimuli (e.g., motion direction) had some jitter (as in a staircase procedure), there was significantly more learning transfer than when there was little feature variance (Xiong, Xie et al., 2016). Consistent with Xiong, Xie et al.'s (2016) study, Green, Kattner, Siegel, Kersten, and Schrater (2015) found that a relatively less varied simple orientation-categorization training task resulted in orientation-specific learning, whereas a more varied orientation-estimation task showed orientation-general learning. Another study (Liang, Zhou, Fahle, & Liu, 2015b) found that even with a staircase method, transfer of motion learning under double-training was not greater than the control condition. However, a meta-analysis (Zhang & Yu, 2016) suggested that the results in Liang et al.'s (2015b) study was not statistically different from those of Zhang et al. (2014) and Xiong, Xie, et al.'s (2016) studies. The meta-analysis exhibited an overall TI of 0.78, comparable to the TIs found in the current study (TI = 0.83 in the double-training condition of Experiment 2, the blue bar in Figure 3e; TI = 0.80 in Experiment 3, the blue bar in Figure 4d; TI = 0.90 in Experiment 4, the solid bar in Figure 5c, and TI = 0.73 in Experiment 5, the solid bar in Figure 6c).

Although motion perceptual learning has been studied for decades, the controversy about the associated brain areas remains. Nishina et al. (2009) suggested that motion perceptual learning occurs in the primary visual cortex in which neurons are particularly sensitive to local motion signals. Besides, the area of V3A has also been suggested to be involved in global motion detection learning (Shibata et al., 2012). On the other hand, electrophysiological studies (Britten, Shadlen, Newsome, & Movshon, 1992; Newsome, Britten, Salzman, & Movshon, 1990) demonstrated that the middle temporal (MT) area in monkeys is particularly sensitive to the motion direction of global motion patterns. This was further confirmed by other studies showing that lesions in the MT and medial superior temporal (MST) areas in monkeys (Newsome & Pare, 1988) and humans (Vaina, Lemay, Bienfang, Choi, & Nakayama, 1990) impaired perception of global motion direction. It could be hypothesized that MT/MST (often referred to as MT+ in humans) are responsible for motion direction discrimination learning. This notion is also supported by psychophysical (Salzman, Britten, & Newsome, 1990) and fMRI studies (Zohary, Celebrini, Britten, & Newsome, 1994). However, it is important to note that motion learning activating some brain areas does not necessarily mean that motion learning takes place in these areas. On the contrary, motion learning can also occur in higher brain areas which send feedback information to these lower visual areas (Mollon & Danilova, 1996). This hypothesis is supported by a neuroimaging study (Law & Gold, 2008) in which motion perceptual learning was accompanied by brain activities in lateral intraparietal (LIP) neurons instead of MT+.

Consistent with Law and Gold’s (2008) study, Zhang and Yang (2014) found that motion discrimination learning transferred significantly (sometimes completely) to the direction opposite to the training direction if participants were passively exposed to the opposite direction. It was suggested that the motion discrimination learning might be a high-level process and that the learning was potentially transferrable rules of re-weighting the motion direction inputs (Zhang et al., 2010). The authors further speculated that brain areas involved in high-level learning are not always functionally connected to the sensory neurons sensitive to other directions, thus leading to direction learning specificity; when there is exposure to motion stimuli in an untrained direction, the functional connectivity with neurons sensitive to the untrained motion direction can be fostered. The top-down connections between high-level learning and low-level visual neurons can be reflected by the ERP P1-N1 changes (Zhang, Cong, Song, & Yu, 2013). Our current findings further suggest that even subconscious stimulation or top-down attention in an untrained motion direction is sufficient for establishing the task specific functional connectivity.

A series of perceptual learning studies with task-irrelevant features had shown that learning only occurred when the irrelevant features were temporally paired with rewards in the trained tasks (Seitz & Watanabe, 2003; Watanabe et al., 2001). The stimulus-reward pairing is suggested to be the mechanism of the learning of task-irrelevant features (Seitz & Watanabe, 2005). However, as discussed earlier, if the untrained and the trained features (e.g., different motion directions) are displayed simultaneously, to enable learning transfer to the untrained feature, the untrained feature should be below the discrimination threshold or awareness so that it will not be suppressed by attention. If the untrained feature is suprathreshold, to avoid attentional suppression, the stimuli carrying the untrained feature should not be presented simultaneously with the trained stimuli (Zhang et al., 2010). The current study provided further evidence that training plus subsequent sub-threshold exposure of untrained features can lead to successful learning transfer.

Last but not least, the top-down attention to the untrained feature had a similar effect. It is worth pointing out that when the bottom-up stimulation/top-down attention and training were separated by days, training preceding the bottom-up stimulation or top-down attention transferred to the untrained feature. However, it is still unclear whether the same effect will be found with a reversed task order (i.e., the bottom-up stimulation/top-down attention before training). According to a previous study (Zhang et al., 2010), this is unlikely because the function of the bottom-up stimulation and the top-down attention is theorized only to consolidate transfer of the learning effect, which should have been achieved beforehand.

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