Contents lists available at ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

Perceptual learning of motion direction discrimination: Location specificity and the uncertain role of dorsal and ventral areas

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ARTICLE INFO

Keywords:
Perceptual learning
Motion direction
External noise
Location Specificity

ABSTRACT

One interesting observation of perceptual learning is the asymmetric transfer between stimuli at different external noise levels: learning at zero/low noise can transfer significantly to the same stimuli at high noise, but not vice versa. The mechanisms underlying this asymmetric transfer have been investigated by psychophysical, neurophysiological, brain imaging, and computational modeling studies. One study (PNAS 113 (2016) 5724–5729) reported that TMS stimulation of dorsal and ventral areas impairs motion direction discrimination of moving dots stimuli at 40% coherent ("noisy") and 100% coherent (zero-noise) levels, respectively. However, after direction training at 100% coherence, only TMS stimulation of the ventral cortex is effective, disturbing direction discrimination at both coherence levels. These results were interpreted as learning-induced change of functional specialization of visual areas. We have concerns with the behavioral data of this study. First, contrary to the report of highly location-specific motion direction learning, our replicating experiment showed substantial learning transfer (e.g., transfer/learning ratio = 81.9% vs. 14.8% at 100% coherence). Second and more importantly, we found complete transfer of direction learning from 40% to 100% coherence, a critical baseline that is missing in this study. The transfer effect suggests that similar brain mechanisms underlie motion direction processing at two coherence levels. Therefore, this study's conclusions regarding the role of dorsal and ventral areas in motion direction processing at two coherence levels, as well as the effects of perceptual learning, are not supported by proper experimental evidence. It remains unexplained how distinct impacts of dorsal and ventral TMS stimulation on motion direction discrimination were observed.

1. Introduction

Perceptual learning leads to better discrimination of fine stimulus differences. As frequently observed, visual perceptual learning is specific to the trained stimulus conditions (e.g., Ball & Sekuler, 1982; Karni & Sagi, 1991; Schoups, Vogels, & Orban, 1995; Crist, Kapadia, Westheimer, & Gilbert, 1997; Yu, Klein, & Levi, 2004). Among various forms of learning specificities, the one originally reported by Dosher and Lu (2005) is unique. They found that orientation learning with a Gabor stimulus at zero external noise can transfer to high external noise. However, the same orientation learning at high external noise transfers little to zero external noise. This asymmetric learning transfer has been replicated in other tasks including motion direction discrimination, disparity discrimination, and Vernier alignment (Lu, Chu, & Dosher, 2006; Chang, Kourtzi, & Welchman, 2013; Chang, Mevorach, Kourtzi, & Welchman, 2014; Xie & Yu, 2019).

Several efforts have been made to understand the mechanisms underlying this asymmetric learning transfer (Chowdhury & DeAngelis, 2008; Lu, Liu, & Dosher, 2010; Chang et al., 2014; Chen, Cai, Zhou, Thompson, & Fang, 2016; Xie & Yu, 2019). Computationally, Lu et al. (2010) suggested that training at high noise, as at zero noise, improves weights of relevant channels, but in a less optimal way. Additionally, training at zero noise is required to achieve more optimal channel reweighting. As a result, only learning at zero noise, in which optimal reweighting of relevant channels has been achieved, can transfer to high noise.

As for the brain mechanisms, Chowdhury and DeAngelis (2008) reported that training of fine disparity discrimination, which relies on ventral areas like V4 and IT, also improves a monkey's coarse discrimination. Moreover, coarse discrimination is no longer affected by temporal chemical inactivation of MT. Because the disparity tuning in MT neurons are unchanged, Chowdhury and DeAngelis (2008) attributed the change to plasticity in downstream decision circuitries.

Consistent with Chowdhury and DeAngelis (2008), Chang et al. (2014)) reported that TMS stimulation of posterior parietal cortex (PPC) and lateral occipital area (LO) impair disparity discrimination at high and zero noise levels, respectively. But after direction training at zero noise, TMS stimulation of LO impaired direction discrimination at both noise levels, and stimulation of PPC became ineffective. However, Chang et al. (2014) concluded that learning changes the weights of the ventral and dorsal areas in direction discrimination, as the downstream decision circuitries. That is, learning reduced the weight of the dorsal cortex in direction discrimination at high noise, and the ventral cortex, which may store the stimulus template, become dominant at both noise levels after training.

Later Chen et al. (2016), the topic of interest of the current study, performed a similar TMS study with motion direction learning. They used a similar experimental design to that of Chang et al. (2014). Specifically, they applied TMS to disrupt the dorsal and ventral areas, and compared the impact of TMS on motion direction thresholds with 100% coherent (zero-noise) and 40% coherent ("noisy") moving-dot stimuli before and after training at zero noise. The results they obtained were also similar. That is, dorsal and ventral stimulation initially affect motion direction thresholds with noisy and zero-noise stimuli, respectively. After training with the zero-noise stimuli, only ventral stimulation affects direction discrimination at both noise or coherence levels. They drew similar conclusions to those of Chang et al. (2014) by stating that "perceptual learning modifies the functional specialization of visual cortical areas", essentially suggesting learning-induced weight change of visual areas in motion direction processing.

Finally, a new development from our lab (Xie & Yu, 2019) shows that learning at high noise can actually transfer to zero noise completely with a double training technique (Xiao et al., 2008; Zhang et al., 2010), despite the 10-time threshold difference at two noise levels. Specifically, Vernier learning at high noise, which initially shows little transfer to zero noise, becomes completely transferable with additional practice of an orientation discrimination task with the same Gabor stimulus at zero noise. A control condition confirms that orientation training by itself has no significant impact on Vernier thresholds. We thus concluded that Vernier learning may occur at a decision stage downstream of dorsal and ventral processing, as previously suggested by Chowdhury and DeAngelis (2008). Moreover, training may improve the conceptual representation of the stimulus feature (Wang et al., 2016), so that learning can eventually transfer completely between different noise levels.

During our research, we started to have concerns with the behavioral data in Chen et al. (2016). First, Chen et al. (2016) reported that motion direction learning transferred little to an untrained hemisphere. In contrast, studies from our lab (Wang, Zhang, Klein, Levi, & Yu, 2014; Xiong, Xie, & Yu, 2016) and other labs (Rokem & Silver, 2010; Zhang & Li, 2010), which also studied motion direction learning with moving dot stimuli, had found substantial learning transfer across hemispheres. For example, approximately 67% of direction learning in Zhang and Li (2010) (their Fig. 1), more than 100% in Rokem and Silver (2010) (the placebo condition in their Fig. 3), and 75% in Wang et al. (2014) (their Fig. 1a) transferred. Second, a crucial behavioral baseline of whether learning can transfer from the noisy condition to the zero-noise condition is missing in Chen et al. (2016). Here learning being specific to the noisy condition is necessary to double-dissociate the inferred roles of dorsal and ventral areas in perceptual learning. Therefore, we decided to run two experiments to address these concerns.

2. Methods

2.1. Observers and experimenters

Twenty-two observers (18–25 years old) with normal or corrected-to-normal vision were recruited. They were new to psychophysical experiments and were naive to the purposes of the study. Informed written consent, which was approved by Peking University Institutional Review Board, was obtained before data collection from each observer. This work was carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

Two experimenters conducted the experiments. The first experimenter (1st author) was aware of the purposes of the study. The second experimenter (2nd author), a new graduate student at the time, was naive. The second experimenter collected more than half of the data (see Results).

2.2. Apparatus and stimuli

The stimuli were generated with Psychtoolbox-3 (Brainard, 1997; Pelli, 1997) and presented on a 21-in SONY G520 CRT monitor (1024 pixel × 768 pixel, 0.39 mm × 0.39 mm per pixel, 120 Hz frame rate, and 46.0 cd/m^2 mean luminance). The screen luminance was linearized by an 8-bit look-up table. Viewing was binocular at a distance of 60 cm with a chin-and-head rest. An Eyelink-1000 eye-tracker (SR Research, Kanata, Ontario, Canada) monitored eye movements. A trial with the eye position deviated from the fixation point for > 2° was immediately aborted and later repeated in the same trial block, which accounted for < 2% of total trials.

The motion stimulus (Fig. 1a) was generated with the same Matlab code obtained from the lab of the last author of Chen et al. (2016), originally for a different purpose. It consisted of 400 black random dots (0.1° × 0.1° each at the minimal luminance) moving at a speed of 37°/s in an invisible 9°-diameter gray circular window. This window was centered on the horizontal meridian 9° to the left or right of the central fixation. In the 100% coherence condition, all dots moved in the same direction (22.5° or 337.5°). In the 40% coherence condition, 40% of the dots, which were randomly chosen, moved in the same direction (22.5° or 337.5°), and the rest were the noise dots moved in random directions.

2.3. Procedure

The experimental procedure followed that of Chen et al. (2016) as closely as possible. Specifically, motion direction discrimination thresholds were measured with a temporal 2AFC QUEST staircase method using the same Matlab code from Chen et al. (2016). In each trial the reference and test (reference direction ± Δdirection) were separately presented in two 200 ms stimulus intervals in a random order, which were separated by a 600 ms inter-stimulus interval (Fig. 1b). A small white fixation point preceded each trial by 1000 ms and stayed through the trial. Observers judged in which interval the random dots moved in a more clockwise direction. Audio feedback was given on incorrect responses. Each QUEST staircase consisted of 40 trials to estimate the direction discrimination threshold at a 75% correct rate. The starting direction difference of the QUEST staircase in both experiments was 12.93°, which was unchanged throughout the experiments for most observers, but was reduced to 8.5° for a few showing lower thresholds.

In the pre- and post-test sessions (Fig. 1c), observers' performance at each condition was estimated with four QUEST staircases. In the training sessions, observers in the first experiment practiced 100% coherence motion stimuli in one hemifield, and in the second experiment practiced 40% coherence motion stimuli in one hemifield. Training lasted for five sessions, with each session consisting of 20 QUEST staircases.

To measure the amount of learning and transfer, the direction discrimination thresholds were measured at two coherence levels and in two hemifields (four conditions) in Experiment 1, and at two coherence levels in the same hemifi

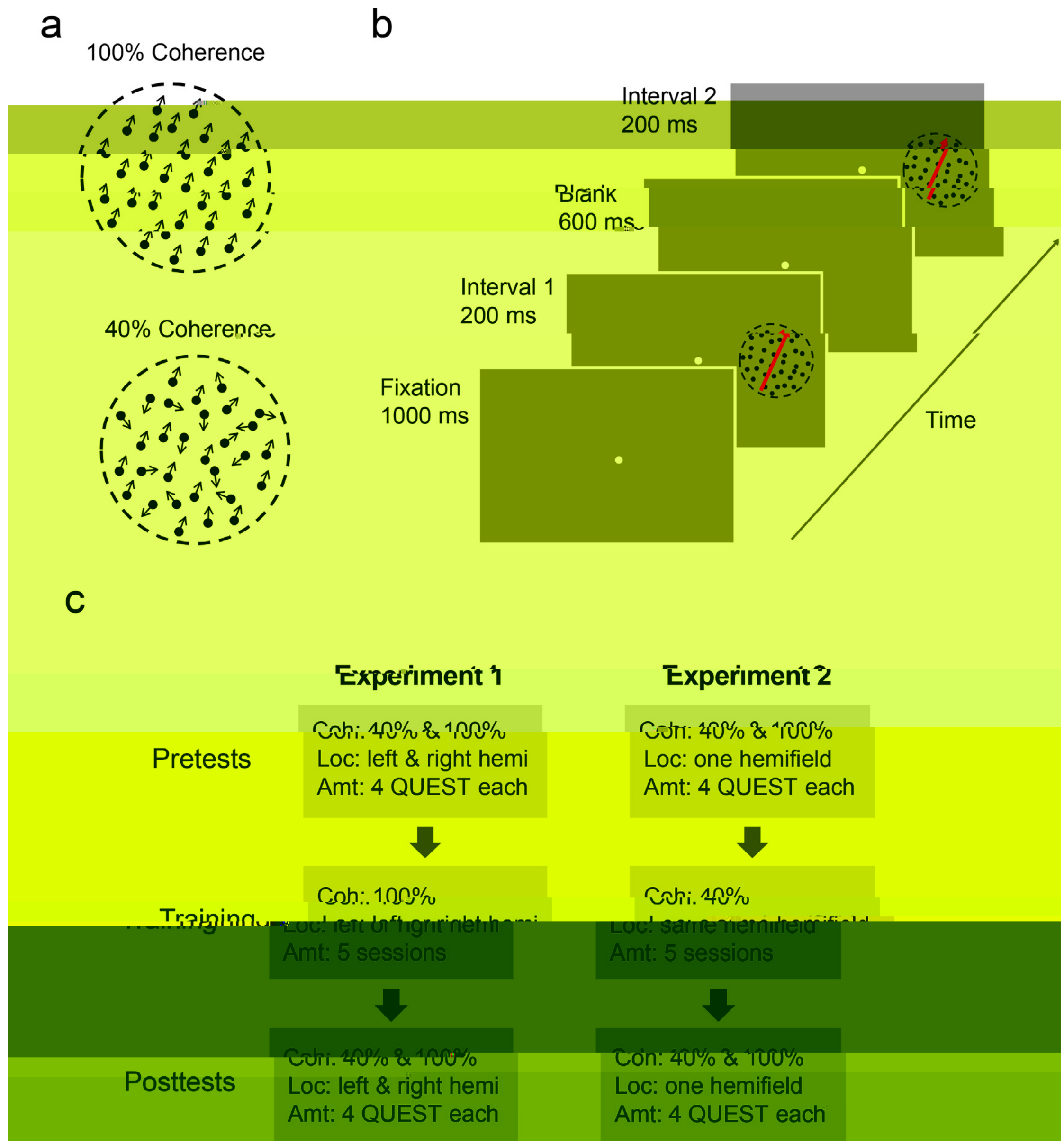

Fig. 1. Stimuli and experimental design. a. Moving dot patterns at two coherence levels. b. Temporal layout of a stimulus trial for motion direction discrimination. c. Pretests, training, and posttest conditions in two experiments.

before data collection on the same day.

2.4. Statistical analysis

Data were analyzed using JASP 0.12.1. The learning and transfer effects were measured by the percent threshold improvements from pre- to post-test sessions, i.e., 100% * ($Threshold_{pre}$ − $Threshold_{post}$) / $Threshold_{pre}$. Individual improvements were first calculated and then averaged to produce the mean improvement and SEM. Threshold improvements were compared against the value 0 with a one-sample *t*-test. Threshold improvements between training and transfer conditions in the same experiment were compared with a two-tailed paired *t*-test, and across experiments were compared with an independent-sample *t*-test. In addition, Bayes factors for the *t*-tests were also calculated.

3. Results

3.1. Experiment I: Transfer of motion direction learning across hemispheres

Chen et al. (2016) reported that perceptual learning of motion direction discrimination at 100% coherence showed little transfer to the untrained hemisphere. Motion direction learning at 100% coherence reduced direction thresholds by 44%. Learning also transferred to 40% coherence in the same hemisphere, reducing direction thresholds by 31%. The transfer/learning ratio was 71%. But in the untrained hemisphere, the performance was improved by approximately 6.5% at 100% coherence, and −4% at 40% coherence (estimated from their Fig. 1D). The corresponding transfer/learning ratios were approximately 14.8% and −9.1%, respectively.

In our replicating experiment (Fig. 2), motion direction training at 100% coherence improved the performance by 34.4 ± 5.3% at 100% coherence ($t_{11} = 6.55$, $p < 0.001$, log Bayes factor [logBF] = 6.43). The learning also transferred to 40% coherence in the same hemisphere, reducing the thresholds by 26.5 ± 4.6% ($t_{11} = 5.78$,

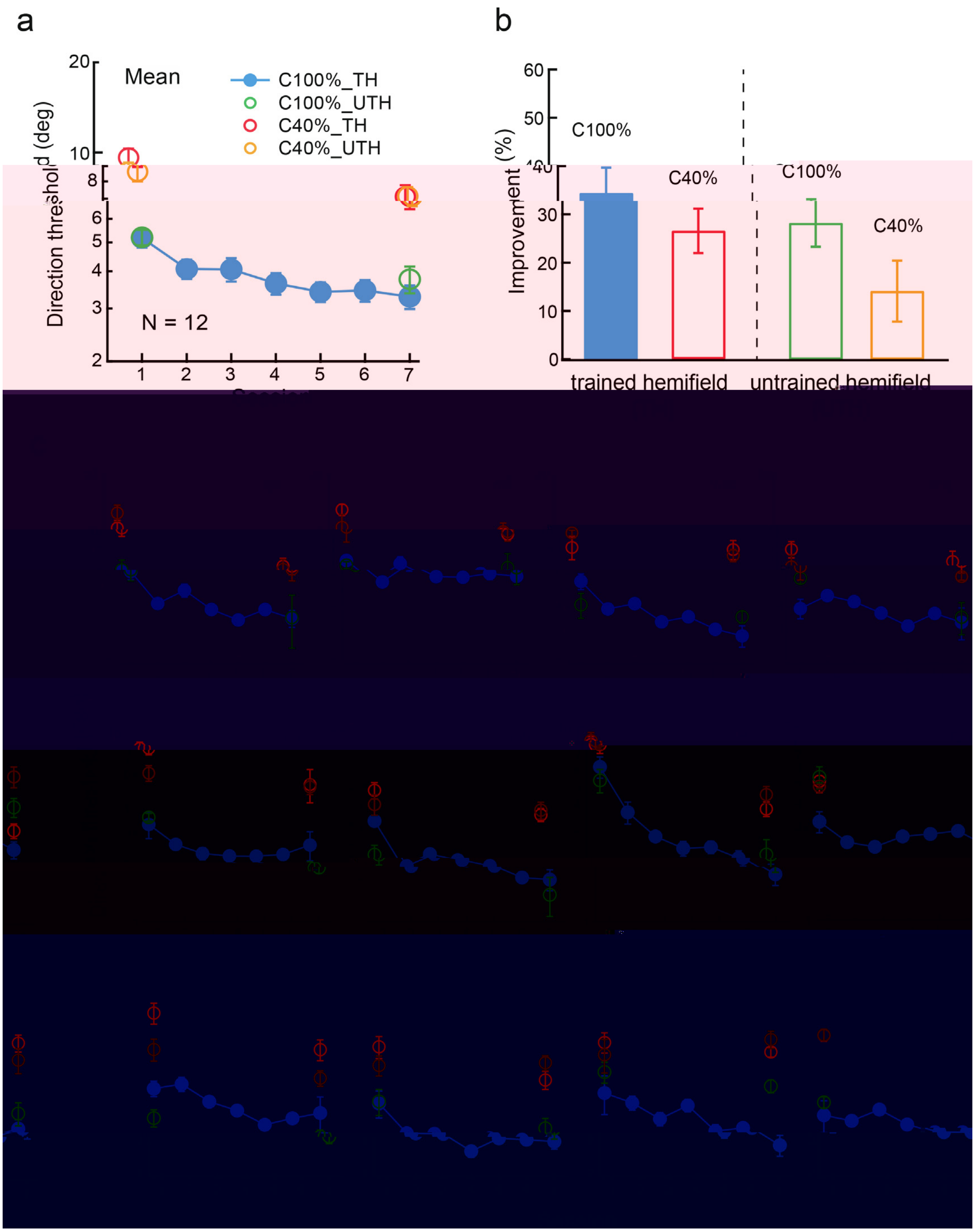

Fig. 2. Perceptual learning of motion direction discrimination and its cross-hemisphere transfer. a. The mean learning curve at 100% coherence, as well as mean pre-/post-training thresholds at 40% coherence in the trained hemisphere, and at 100% and 40% coherence in the untrained hemisphere. b. A summary of learning and transfer. c. Individual results. Data of last 7 observers were collected by a naive experimenter. Error bars indicate ± 1 standard error of the mean.

$p < 0.001$, logBF = 5.49). The corresponding transfer/learning ratio was 77.0%, similar to 71% in Chen et al. (2016). However, training also improved the performance in the untrained hemisphere by 28.2 ± 4.9% at 100% coherence ($t_{11} = 5.73$, $p < 0.001$, logBF = 5.42), and by 14.1 ± 6.4% at 40% coherence ($t_{11} = 2.21$, $p = 0.049$, logBF = 0.52). The latter improvement was moderate with a logBF of 0.52 (Andraszewicz, Scheibehenne, Rieskamp, Grasman, Verhagen, & Wagenmakers, 2015). The corresponding transfer/learning ratios were 81.9% and 41.0%, respectively, in contrast to the corresponding ratios of 14.8% and −9.1% in Chen et al. (2016). Moreover, there was no significant statistical difference between learning and transfer at the same 100% coherence level ($t_{11} = 1.22$, $p = 0.247$, logBF = −0.64) where the training and transfer stimuli were identical.

Our replicating experiment thus revealed substantial learning transfer across hemispheres, especially at the same 100% coherence level where the difference between learning and transfer was statistically insignificant. The results contradict the high location specificity of motion direction learning in Chen et al. (2016), despite the use of nearly identical stimuli and procedure.

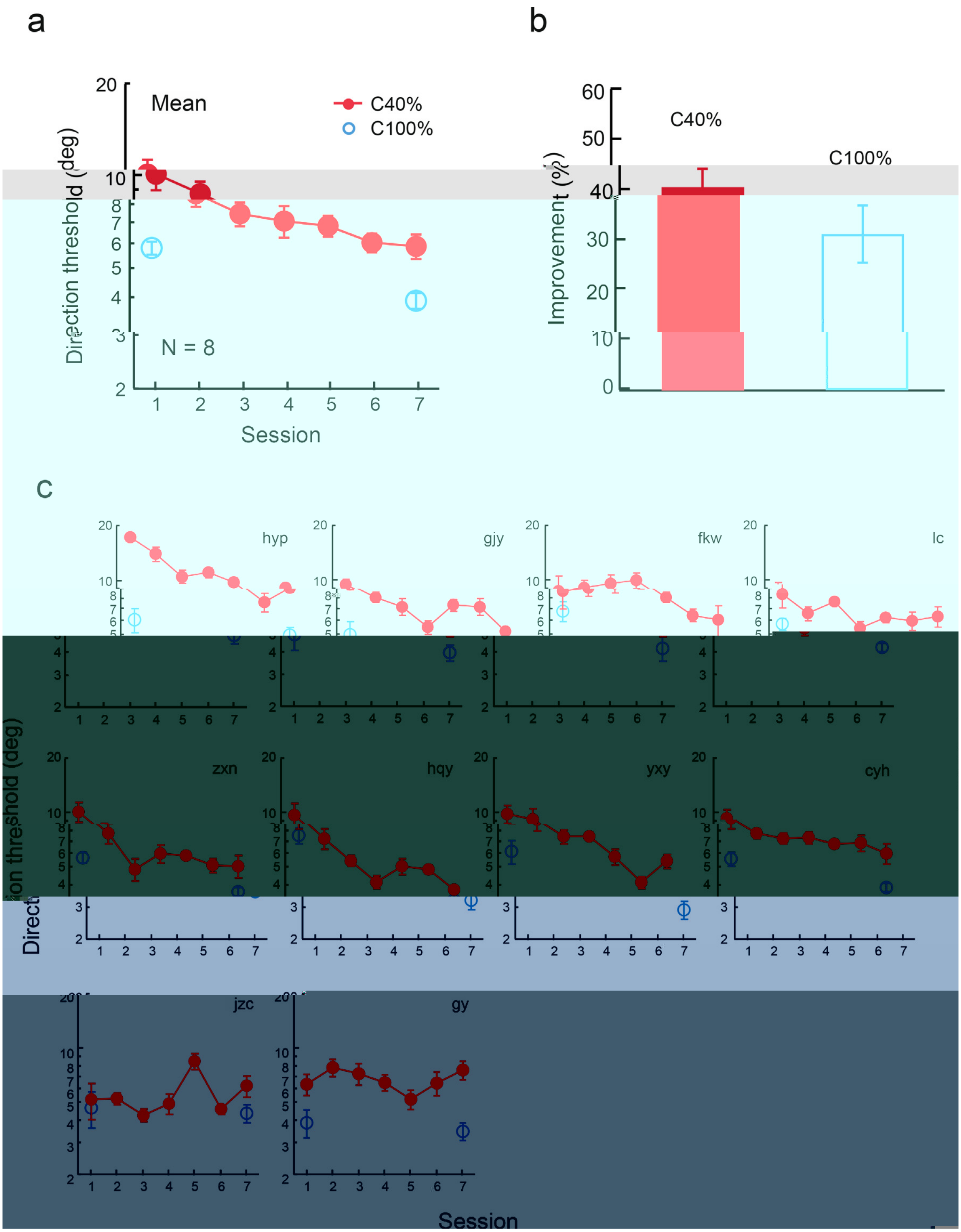

Fig. 3. Transfer of motion direction learning from "noisy" 40% coherent stimuli to zero-noise 100% coherent stimuli. a. The mean learning curve at 40% coherence, as well as the mean pre-/post-training thresholds at 100% coherence at the same location. b. A summary of learning and transfer. c. Individual results. Data of last 6 observers were collected by a naive experimenter. Error bars indicate ±1 standard errors of the mean.

3.2. Experiment II: Transfer of motion direction learning from noisy to zero-noise stimuli

In an earlier TMS study, Chang et al. (2014) reported that disparity learning at high noise did not transfer to zero noise with their stimuli. This behavioral baseline is critical because it double-dissociates the different roles of dorsal and ventral areas in disparity processing at high and zero noise levels inferred from TMS results. However, a similar baseline regarding the specificity/transfer of motion direction learning from "noisy" 40% coherence to zero-noise 100% coherence is missing in Chen et al. (2016). Because of its importance to the interpretation of the TMS data in Chen et al. (2016), we decided to collect data for this baseline condition.

We had ten new observers practice motion direction learning at 40% coherence (Fig. 3). Two observers who showed negative improvements (Fig. 3c, bottom two observers) were excluded from data analysis because we were interested in how much learning could transfer. The remaining results showed that training improved motion direction discrimination not only at 40% coherence by 40.5 ± 3.7% ($t_7 = 10.88$, $p < 0.001$, logBF = 7.37), but also at 100% coherence by 31.1 ± 5.7% ($t_7 = 5.46$, $p < 0.001$, logBF = 3.76) at the same location. Moreover, for motion direction at 100% coherence, the improvements through learning transfer here was nearly identical to that through direct training in Experiment 1 (31.1% vs 34.4%; $t_{18} = 0.41$, $p = 0.685$, logBF = -0.85), suggesting complete learning transfer. Therefore, with the current stimulus configuration, the expected baseline of no learning transfer from 40% to 100% coherence, or from noisy to zero-noise motion stimuli, cannot be established.

4. Discussion

In this study we demonstrated that motion direction learning with the stimulus configuration of Chen et al. (2016) transfers substantially across hemispheres, especially at the 100% coherence level where the learning and transfer stimuli are identical (Fig. 2). More importantly, we collected the missing baseline data, demonstrating complete learning transfer from 40% to 100% coherence (Fig. 3). The latter result suggests that motion direction at two noise or coherence levels are likely processed by similar brain mechanisms. Therefore, the inferred roles of dorsal and ventral areas in motion direction processing, as well as the effects of perceptual learning on these roles, may not be properly double-dissociated by behavioral evidence in Chen et al. (2016). It remains unexplained why distinct impacts of dorsal and ventral TMS stimulation on motion direction discrimination at two coherence levels were observed by these researchers.

Although the stimulus configuration, testing procedure, and experimental design of Experiment 1 were nearly identical to those in Chen et al. (2016), there was one notable exception. In Chen et al. (2016), after the pretests, TMS stimulation were performed and the same psychophysical tests were repeated. As shown in their Fig. 1D, these additional procedures did not impede learning at the trained 100% coherence (44% vs 34% improvement) and learning transfer to the untrained 40% coherence in the same hemisphere (transfer/learning ratio = 71% vs 70%). This was simply because training was conducted after the impacts of TMS stimulation were long gone. For the same reason, these additional procedures were not expected to affect learning transfer to stimuli in the untrained hemifield either.

Perceptual learning results are often affected by procedural learning. In Experiment 1, as in Chen et al. (2016), each observer before data collection practiced two staircases for each condition for a total of 320 trials (4_cond × 2_staircase × 40 trials/staircase), which was sufficient to saturate procedural learning. In Experiment 2, one staircase was practiced for each of two conditions (2_cond × 1_staircase × 40 trials/staircase = 80 trials). After this initial practice, the pretests formally started, and the threshold changed from the first to the fourth staircase by −9.3% (from 10.11 ± 1.38 to 11.04 ± 1.40) at 40% coherence, and by 15% (from 5.97 ± 0.52 to 5.05 ± 0.45) at 100% coherence. Therefore, evidence for the impacts of possible procedural learning was inconsistent even within the pretests after 80 trials of practice. It is thus safe to conclude that perceptual learning results in Experiment 2 have not been significantly contaminated by procedural learning.

High location specificity of motion direction learning has been reported previously (Ball and Sekuler, 1982, 1987; Liu, 1999). So why did motion direction learning fail to show much location specificity here? It might depend on how direction thresholds are measured. Mollon and Danilova (1996) once pointed out that location specificity in perceptual learning may result from an observer's "learning about the optical features of his retinal image; about the local topography of his receptor mosaic; and about the specific wiring of individual neurons within his visual pathway". As we have argued previously (Xiong et al., 2016), when training is performed with the direction threshold measured by a method of same-different comparisons with a pair of fixed stimuli, as in early studies by Ball and Sekuler (1982, 1987) and Liu (1999), an observer might be able to learn what exactly these local cues or "idiosyncracies" (Mollon & Danilova, 1996) are, which could result in over-fitting (Sagi, 2011) and thus location specificity. To support this argument, we demonstrated that if the direction difference of a stimulus pair is kept constant, but their individual directions are slightly jittered trial by trial to discourage the use of potential local cues, learning becomes significantly more transferable to a new hemisphere (Xiong et al., 2016). A standard QUEST staircase varies the stimulus direction trial by trial, which also discourages learning of local cues, so that motion learning is not much location specific, as shown in Experiment 1 and in previous studies (Rokem & Silver, 2010; Zhang & Li, 2010; Wang et al., 2014; Xiong et al., 2016). In fact, we started the current study because the high location specificity reported by Chen et al. (2016) challenged the above predictions presented in Xiong et al. (2016). Therefore, we felt it necessary to repeat Chen et al.'s experiments to double check these predictions.

Why did motion direction learning transfer from noisy 40% coherence to zero-noise 100% coherence? The answer may lie in the fact that 40% coherence in Chen et al. (2016) is not noisy enough. In the original study by Dosher and Lu (2005), the contrast threshold at high noise were about 10 times of the threshold at zero noise. So was the difference of Vernier threshold at high versus zero noise levels in our study (Xie & Yu, 2019), which was also about 10 to 1. However, the motion direction threshold at 40% coherence were only about twice as high as that at 100% coherence (Figs. 2 and 3). Therefore, the 40% coherence condition was still near the low-noise end of the threshold versus noise-level function, where training could still optimize the weights of relevant channels according to Lu et al. (2010), and learning was thus transferable to 100% coherence.

CRediT authorship contribution statement

Xin-Yu Xie: Investigation, Formal analysis, Writing - original draft. **Xing-Nan Zhao:** Investigation. **Cong Yu:** Conceptualization, Formal analysis, Writing - review and editing.

Acknowledgements

This study was supported by funds from Peking-Tsinghua Center for Life Sciences, Peking University (CY) and a Natural Science Foundation of China grant 31900799 (XYX). We thank the comments and suggestions from colleagues who also study perceptual learning.

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