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

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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 stimulus 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 rTMS stimulations of dorsal and ventral areas impair motion direction discrimination of moving dot stimuli at 40% coherent ("noisy") and 100% coherent (zero-noise) levels, respectively. However, after direction training at 100% coherence, only rTMS stimulation of the ventral cortex is effective, disturbing direction discrimination at both coherence levels. These results were interpreted as learning-induced changes of functional specializations 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 roles 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 why distinct impacts of dorsal and ventral rTMS stimulations 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. Additional training at zero noise is required to achieve optimal channel re-weighting. As a result, only learning at zero noise, in which optimal weighting 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 changes to plasticity in downstream decision circuitries.

Consistent with Chowdhury and DeAngelis (2008), Chang et al. (2014)) reported that rTMS stimulations of posterior parietal cortex (PPC) and lateral occipital area (LO) impair disparity discrimination at

high and zero noise levels, respectively. But after disparity training at zero noise, rTMS stimulation of LO impairs disparity discrimination at both noise levels, and stimulation of PPC becomes ineffective. However, Chang et al. (2014) concluded that learning changes the weights of the ventral and dorsal areas in disparity discrimination, rather than downstream decision circuitries. That is, learning reduced the weight of the dorsal cortex in disparity discrimination at high noise, and the ventral cortex, which may store the stimulus template, becomes dominant at both noise levels after training.

Later Chen et al. (2016), the topic of interest of the current study, performed a similar rTMS study with motion direction learning. They used a similar experimental design to that of Chang et al. (2014). Specifically, they applied rTMS to disturb the dorsal and ventral areas, and compared the impacts of rTMS 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 stimulations initially affect motion direction thresholds with noisy and zero-noise stimuli, respectively. After training with the zero-noise stimuli, only ventral stimulations affect 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 specializations of visual cortical areas", essentially suggesting learning-induced weight changes 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 transferrable 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). l2o,over, 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 transfers little to an untrained hemisphere. In contrary, 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 naïve 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 purpose of the study. The second experimenter (2nd author), a new graduate student at the time, was naïve. 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 pixel size, 120 Hz frame rate, and 46.0 cd/m² 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) moved 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 as 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). same6(al.)ametria
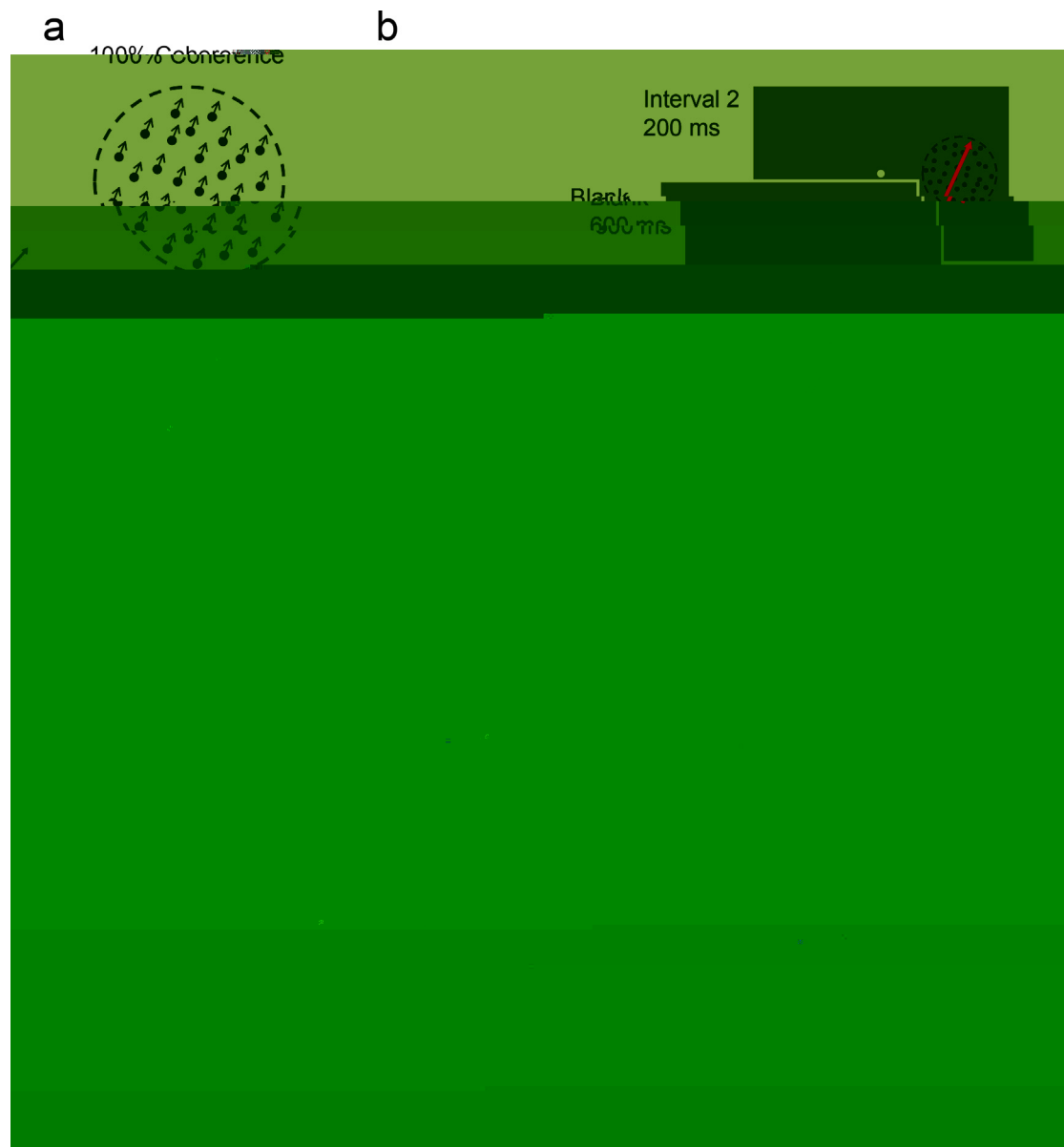
Fig. 1. Stimuli and experimental design. a. Moving dot patterns at two coherence levels. b. Temporal layout of a stimulus trial for motion direction discrimination. c. Pretest, training, and posttest conditions in two experiments.

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., $100\% * (\text{Threshold}_{pre} - \text{Threshold}_{post}) / \text{Threshold}_{pre}$. 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-samples *t*-test. In addition, Bayes factors for these 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% ($t_{11} = 5.78$,
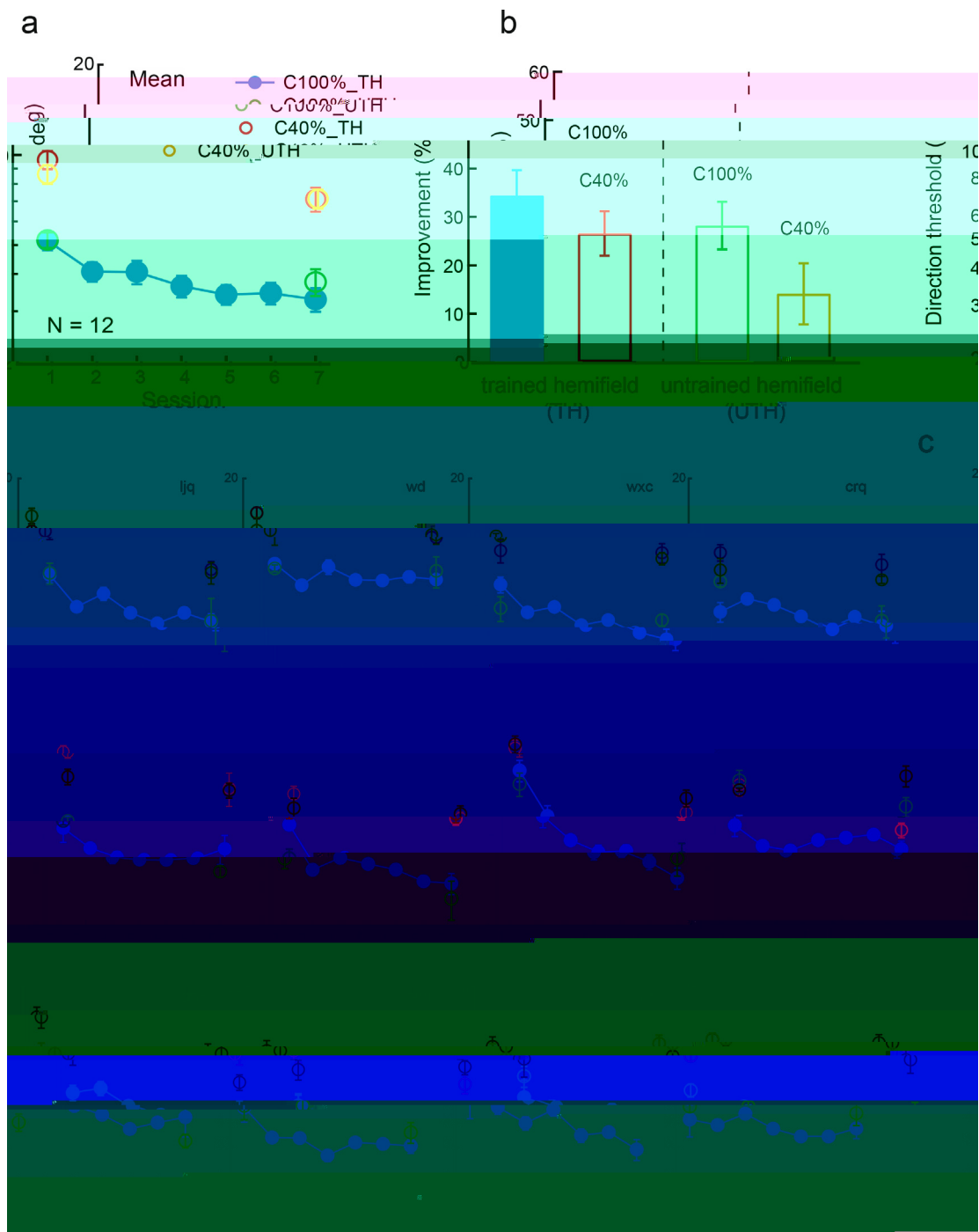
Fig. 2. Perceptual learning of motion direction discrimination and its cross-hemisphere transfer. a. The mean learning curve at 100% coherence, as well as mean pre-/post-training thresholds at 40% coherence in the trained hemisphere, and at 100% and 40% coherences in the untrained hemisphere. b. A summary of learning and transfer. c. Individual results. Data of last 7 observers were collected by a naïve 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, Grasman, Verhagen, & Wagenmakers, 2015). The corresponding transfer/learning ratios were 81.9% and 41.0%, respectively, in sharp 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 reveals substantial learning transfer across hemispheres, especially at the same 100% coherence level where the difference between learning and transfer was statistically insignificant. These results contradict the high location specificity of motion direction learning in Chen et al. (2016), despite the use of nearly identical stimuli and procedure.
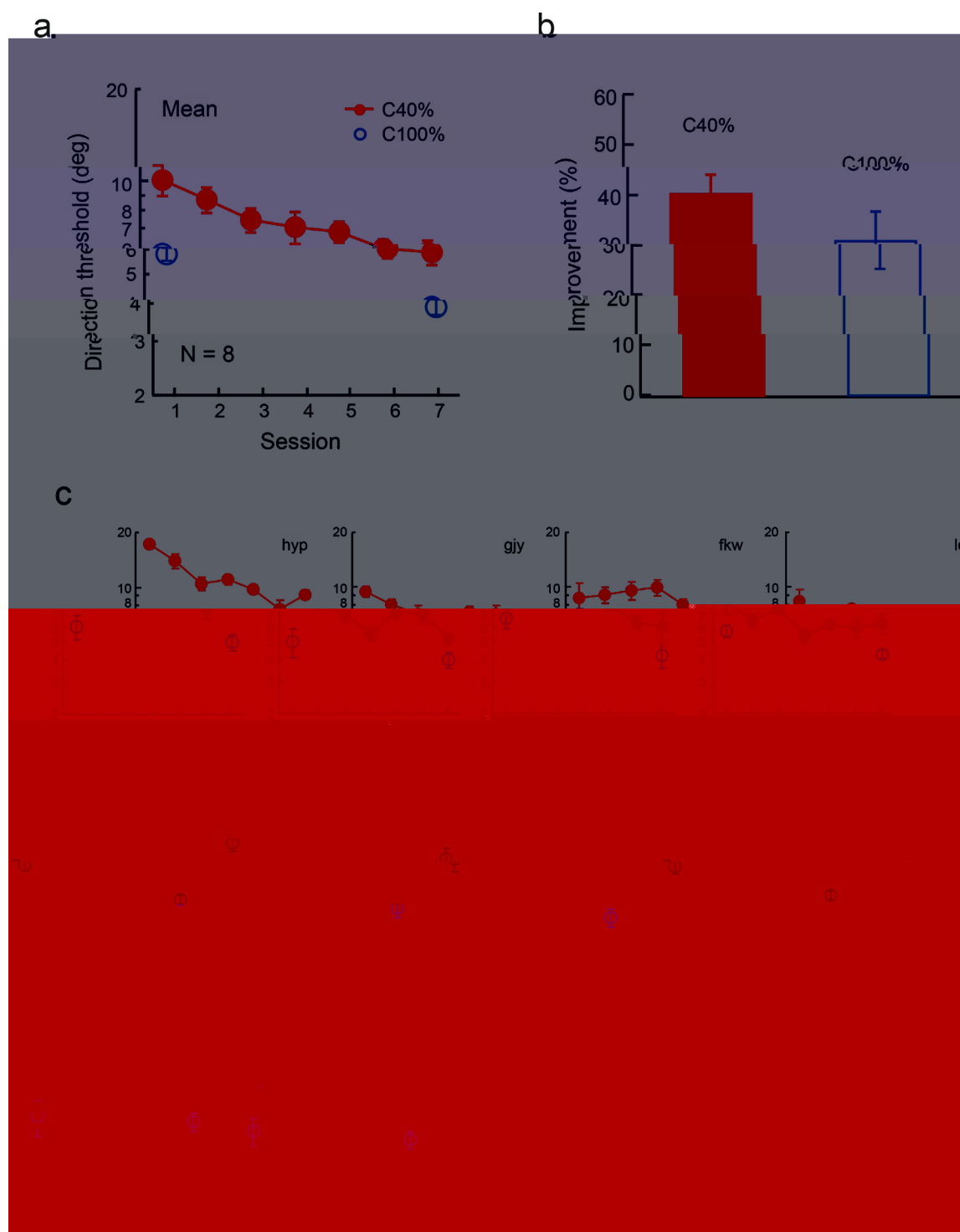
Fig. 3. Transfer of motion direction learning from "noisy" 40% coherent stimuli to zero-noise 100% coherent stimuli. a. The mean learning curve at 40% coherence, as well as the mean pre-/post-training thresholds at 100% coherence at the same location. b. A summary of learning and transfer. c. Individual results. Data of last 6 observers were collected by a naïve experimenter. Error bars indicate ± 1 standard error of the mean.

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

In an earlier rTMS 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 rTMS 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 interpretations of the rTMS 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 improvement (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 $40.5 \pm 3.7\%$ ($t_7 = 10.88$, $p < 0.001$, logBF = 7.37), but also at 100% coherence by $31.1 \pm 5.7\%$ ($t_7 = 5.46$, $p < 0.001$, logBF = 3.76) at the same location. Moreover, for motion direction at 100% coherence, the improvement 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 configurations, 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 rTMS stimulations 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 stimulations 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 our 34% improvements) and learning transfer to the untrained 40% coherence in the same hemisphere (transfer/learning ratio = 71% vs our 70%). This was simply because training was conducted after the impacts of TMS stimulations 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 thresholds changed from the first to the fourth staircase by −9.3% (from $10.11° \pm 1.38°$ to $11.04° \pm 1.40°$) at 40% coherence, and by 15% (from $5.97° \pm 0.52°$ to $5.05° \pm 0.45°$) at 100% coherence. Therefore, evidence for the impact 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 pathways". As we have argued previously (Xiong et al., 2016), when training is performed with the direction thresholds measured by a

method of same-different comparison 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 "idiosyncrasies" (Mollon & Danilova, 1996) are, which could result in overfitting (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 transferrable to a new hemisphere (Xiong et al., 2016). A standard or 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 experiment 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 thresholds at high noise were about 10 times of the thresholds at zero noise. So was the difference of Vernier thresholds at high vs zero noise levels in our study (Xie & Yu, 2019), which was also about 10 to 1. However, the motion direction thresholds at 40% coherence were only about twice as high as those at 100% coherence (Figs. 2 and 3). Therefore, the 40% coherence condition was still near the low-noise end of the threshold vs noise-level function, where training could still optimize the weights of relevant channels according to Lu et al. (2010), and learning was thus transferrable 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.

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