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 roles 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 dot 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 changes of functional specialization of visual areas. We have concerns with the behavioral data of this study. Firstly, 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 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 cannot transfer to low or zero external noise. This asymmetric learning transfer has been replicated in other tasks including motion direction discrimination, dot spacing 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 opposed to zero noise, improves reweighting of relevant channels, but in a less optimal way. Additional training at zero noise is required to achieve 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) showed 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 chemical inactivation of MT. Because the disparity tuning in MT neurons are unchanged, Chowdhury and DeAngelis (2008) attributed the changes to late circuits in downstream decision circuits.

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 e o noi e le el , e ec i el . B af e di a i aining a e o noi e, TMS im la ion of LO im ai di a i di c imina ion a bo h noi e le el , and im la ion of PPC become ineffec i e. Ho e e , Chang e al. (2014) concl ded ha lea ning change he eigh of he en al and do al a ea in di a i di c imina ion, a he han do n eam deci ion ci c i ie . Tha i , lea ning ed ced he eigh of he do al co e in di a i di c imina ion a high noi e, and he en al co e , hich ma o e he im l em la e, become dominan a bo h noi e le el af e aining.

La e Chen e al. (2016), he o ic of in e e of he c en d , e fo med a imila TMS d i h mo ion di ec ion lea ning. The ed a imila e e imen al de ign o ha of Chang e al. (2014). S ecificall , he a lied TMS o di b he do al and en al a ea , and com a ed he im ac of TMS on mo ion di ec ion h e hold i h 100% cohe en (e o noi e) and 40% cohe en ("noi ") mo ing-do im li befo e and af e aining a e o noi e. The e l he ob ained e e al o imila . Tha i , do al and en al im la ion ini iall affec mo ion di ec ion h e hold i h noi and e o-noi e im li, e ec i el . Af e aining i h he e o-noi e im li, onl en al im la ion affec di ec ion di c imina ion a bo h noi e o cohe ence le el . The d e imila concl ion o ho e of Chang e al. (2014) b a ing ha " e ce al lea ning modifie he f nc ional eciali a ion of i al co ical a ea ", e en iall gge ing lea ning-ind ced eigh change of i al a ea in mo ion di ec ion oce ing.

Finall , a ne de elo men f om o lab (Xie & Y , 2019) ho ha lea ning a high noi e can ac all an fe o e o noi e com le el i h a do ble aining echni e (Xiao e al., 2008; Zhang e al., 2010), de i e he 10 ime h e hold diffe ence a o noi e le el . S ecificall , Ve nie lea ning a high noi e, hich ini iall ho li le an fe o e o noi e, become com le el an fe able i h addi ional ac ice of an o ien a ion di c imina ion a k i h he ame Gabo im l a e o noi e. A con ol condi ion confi m ha o ien a ion aining b i elf ha no ignifican im ac on Ve nie h e hold . We h concl ded ha Ve nie lea ning ma occ a a deci ion age do n eam of do al and en al oce ing a e io l gge ed b Cho dh and DeAngeli (2008). Mo eo e , aining ma im o e he conce al e e en a ion of he im l fea e (Wang e al., 2016), o ha lea ning can e en all an fe com le el be een diffe en noi e le el .

D ing o e ea ch, e a ed o ha e conce n i h he beha io al da a in Chen e al. (2016). Fi , Chen e al. (2016) e o ed ha mo ion di ec ion lea ning an fe li le o an n ained hemi he e. In con a , die f om o lab (Wang, Zhang, Klein, Le i, & Y , 2014; Xiong, Xie, & Y , 2016) and o he lab (Rokem & Sil e , 2010; Zhang & Li, 2010), hich al o died mo ion di ec ion lea ning i h mo ing do im li, had fo nd b an ial lea ning an fe ac o hemi he e . Fo e am le, a o ima el 67% of di ec ion lea ning in Zhang and Li (2010) (hei Fig. 1), mo e han 100% in Rokem and Sil e (2010) (he lacebo condi ion in hei Fig. 3), and 75% in Wang e al. (2014) (hei Fig. 1a) an fe ed. Second, a c cial beha io al ba eline of he he lea ning can an fe f om he noi condi ion o he e o-noi e condi ion i mi ing in Chen e al. (2016). He e lea ning being ecific o he noi condi ion i nece a o do ble-di ocia e he infe ed ole of do al and en al a ea in e ce al lea ning. The efo e, e decided o n o e e imen o add e he e conce n .

2. Methods

2.1. Observers and experimenters

T en - o ob e e (18–25 ea old) i h no mal o co ec ed-o-no mal i ion e e ec i ed. The e e ne o cho h ical e e imen and e e na e o he o e of he d . Info med i en con en , hich a a o ed b Peking Uni e i In i ional Re ie Boa d, a ob ained befo e da a collec ion f om each ob e e . Thi o k a ca ied o in acco dance i h he Code of E hic of he Wo ld Medical A ocia ion (Decla a ion of Hel inki).

T o e e imen e cond c ed he e e imen . The fi e e i-men e (1 a ho) a a a e of he o e of he d . The econd e e imen e (2nd a ho), a ne g ad a e den a he ime, a na e. The econd e e imen e collec ed mo e han half of he da a (ee Re l).

2.2. Apparatus and stimuli

The im li e e gene a ed i h P ch oolbo -3 (B aina d, 1997; Pelli, 1997) and e en ed on a 21-in SONY G520 CRT moni o (1024 i el 768 i el, 0.39 mm 0.39 mm i el i e, 120 H f ame a e, and 46.0 cd/m^2 mean l minance). The c een l minance a linea i ed b an 8-bi look- able. Vie ing a binoc la a a di ance of 60 cm i h a chin-and-head e . An E elink-1000 e e- acke (SR Re ea ch, Kana a, On a io, Canada) moni o ed e e mo emen . A ial i h he e e o i ion de ia ed f om he fi a ion oin fo > 2 a immedia el abo ed and la e e ea ed in he ame ial block, hich acco n ed fo < 2% of o al ial .

The mo ion im l (Fig. 1a) a gene a ed i h he ame Ma lab code ob ained f om he lab of he la a ho of Chen e al. (2016), o iginall fo a diffe en o e. I con i ed of 400 black andom do (0.1 0.1 each a he minimal l minance) mo ed a a eed of 37 / in an in i ible 9 diame e g a ci c la indo . Thi indo a cen e ed on he ho i on al me idian 9 o he lef o igh of he cen al fi a ion. In he 100% cohe ence condi ion, all do mo ed in he ame di ec ion (22.5 o 337.5). In he 40% cohe ence condi ion, 40% of he do , hich e e andoml cho en, mo ed in he ame di ec ion (22.5 o 337.5), and he e a he noi e do mo ed in andom di ec ion .

2.3. Procedure

The e e imen al oced e follo ed ha of Chen e al. (2016) a clo el a o ible. S ecificall , mo ion di ec ion di c imina ion h e hold e e mea ed i h a em o al 2AFC QUEST ai ca e me hod ing he ame Ma lab code f om Chen e al. (2016). In each ial, he efe ence and e (efe ence di ec ion Δdi ec ion) e e e a a el e en ed in o 200 m im l in e al in a andom o de , hich e e e a a ed b a 600 m in e - im l in e al (Fig. 1b). A mall hi e fi a ion oin eceded each ial b 1000 m and a ed h o gh he ial. Ob e e j dged in hich in e al he andom do mo ed in a mo e clock i e di ec ion. A di o feedback a gi en on inco ec e on e . Each QUEST ai ca e con i ed of 40 ial , o e ima e he di ec ion di c imina ion h e hold a a 75% co ec a e. The a ing di ec ion diffe ence of he QUEST ai ca e in bo h e imen a 12.93 , hich a nchanged h o gho he e e imen fo mo ob e e , b a ed ced o 8.5 fo a fe ho ing lo e h e hold .

In he e- and o - e e ion (Fig. 1c), ob e e e fo mance a each condi ion a e ima ed i h fo QUEST ai ca e . In he aining e ion, ob e e in he fi e e imen ac iced 100% co-he ence mo ion im li in one hemifield, and in he econd e e imen ac iced 40% cohe ence mo ion im li in one hemifield. T aining la ed fo fi e e ion , i h each e ion con i ing of 20 QUEST ai ca e .

To mea e he amo n of lea ning and an fe , he di ec ion di c imina ion h e hold e e mea ed a o cohe ence le el and in o hemifield (fo e condi ion) in E e imen 1, and a o co-he ence le el in he ame hemifield (o e condi ion)

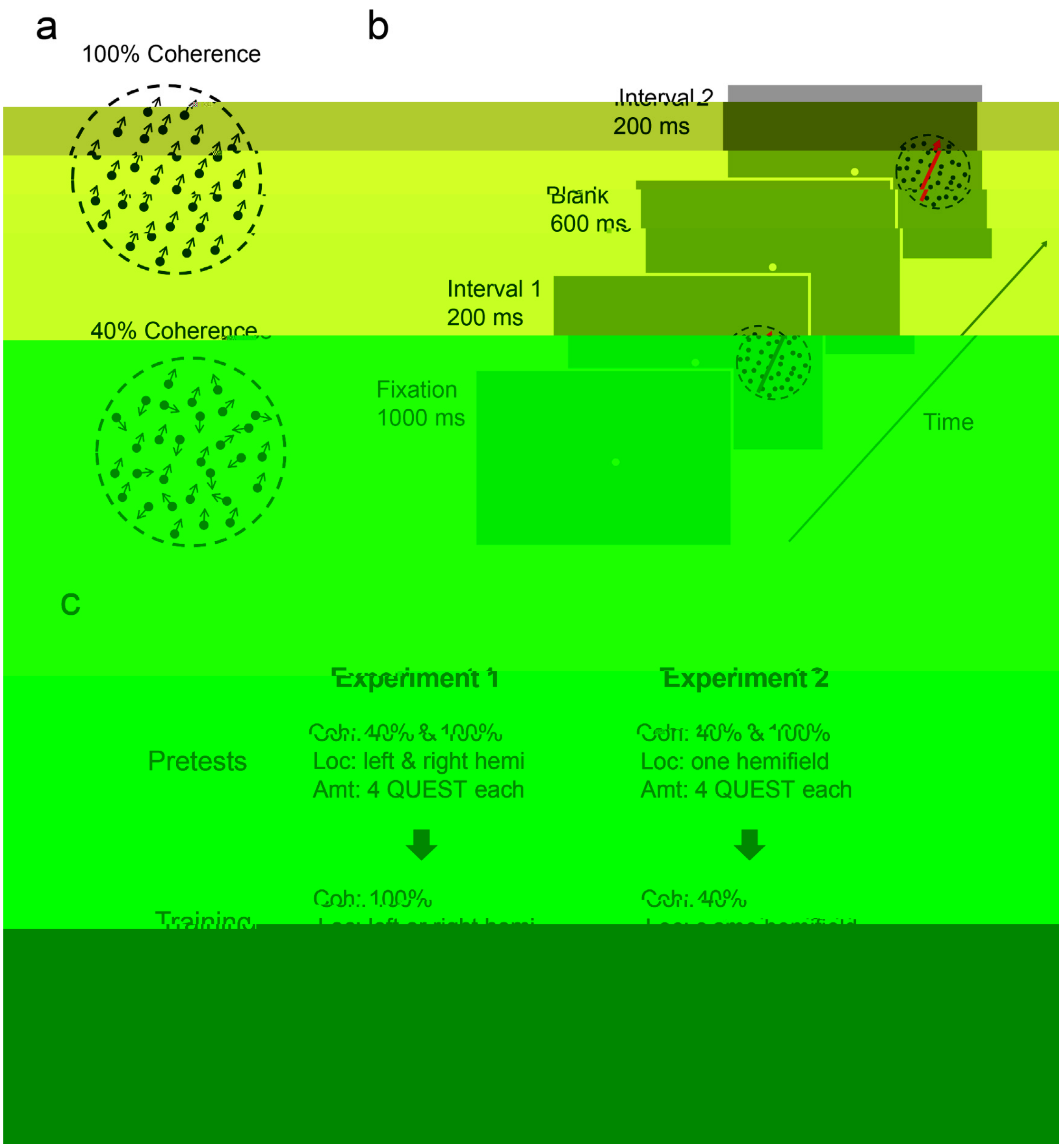

Fig. 1. S im li and e e imen al de ign. a. Mo ing do a e n a o cohe ence le el . b. Tem o al la o of a im l ial fo mo ion di ec ion di c imina ion. c. P e e , aining, and o e condi ion in o e e imen .

befo e da a collec ion on he ame da .

2.4. Statistical analysis

Da a e e anal ed ing JASP 0.12.1. The lea ning and an fe effec e e mea ed b he e cen h e hold im o emen f om e o o - e e ion , i.e., 100% * (Th e hold – Th e hold) / Th e hold . Indi id al im o emen e e fi calc la ed and hen a e aged o od ce he mean im o emen and SEM. Th e hold im o emen e e com a ed again he al e 0 i h a one- am le t-e . Th e hold im o emen be een aining and an fe condi ion in he ame e imen e e com a ed i h a o- ailed ai ed t- e , and ac o e e imen e e com a ed i h an inde enden - am le t-e . In addi ion, Ba e fac o fo he e - e e e al o calc la ed.

3. Results

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

Chen e al. (2016) e o ed ha e ce al lea ning of mo ion di ec ion di c imina ion a 100% cohe ence ho ed li le an fe o he n ained hemi he e. Mo ion di ec ion lea ning a 100% cohe ence ed ced di ec ion h e hold b 44%. Lea ning al o an fe ed o 40% cohe ence in he ame hemi he e, ed cing di ec ion h e hold b 31%. The an fe /lea ning a io a 71%. B in he n ained hemi he e, he e fo mance a im o ed b a o ima el 6.5% a 100% cohe ence, and − 4% a 40% cohe ence (e ima ed f om hei Fig. 1D). The co e onding an fe /lea ning a io e e a o ima el 14.8% and − 9.1%, e ec i el .

In o e lica ing e e imen (Fig. 2), mo ion di ec ion aining a 100% cohe ence im o ed he e fo mance b 34.4 5.3% a 100% cohe ence ($_{11}$ = 6.55, < 0.001, log Ba e fac o [logBF] = 6.43). The lea ning al o an fe ed o 40% cohe ence in he ame hemi he e, ed cing he h e hold b 26.5 4.6% ($_{11}$ = 5.78,

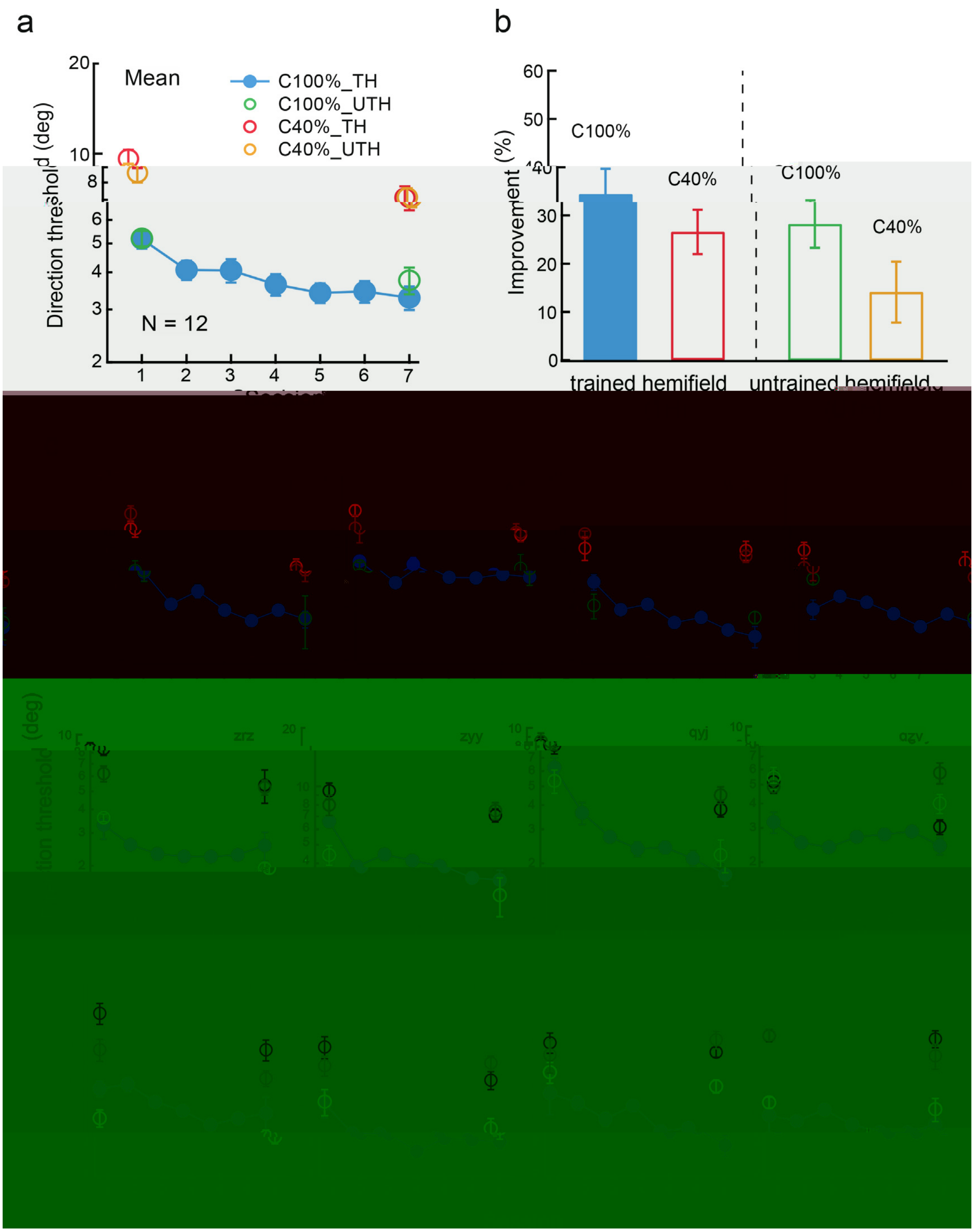

Fig. 2. Perceptual learning of motion direction discrimination and its cross-hemisphere transfer. a. The mean learning curve at 100% coherence, as well as mean pre-/post-training thresholds at 40% coherence in the trained hemifield, and at 100% and 40% coherence in the untrained hemifield. b. A summary 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 hemifield 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) when the training and transfer stimuli were identical.

Our replicating experiment thus revealed substantial learning transfer across hemifields, 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.

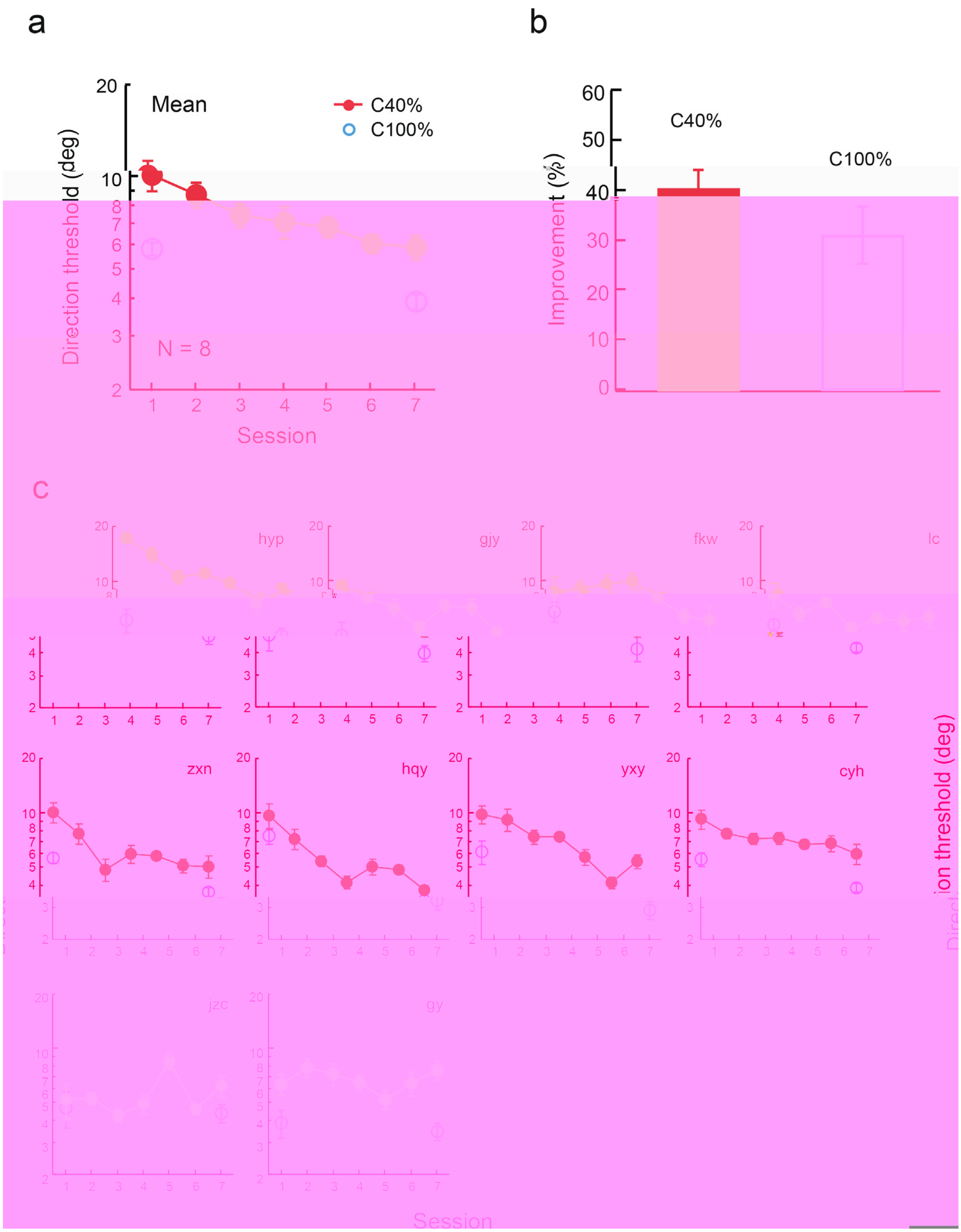

Fig. 3. T an fe of mo ion di ec ion lea ning f om “noi ” 40% cohe en im li o e o-noi e 100% cohe en im li. a. The mean lea ning c e a 40% cohe ence, a ell a he mean e-/ o - aining he hold a 100% cohe ence a he ame loca ion. b. A mma of lea ning and an fe . c. Indi id al e l . Da a of la 6 ob e e e e collec ed b a na e e e imen e . E o ba indica e 1 anda d e o of he mean.

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

In an ea lie TMS d , Chang e al. (2014) e o ed ha di a i lea ning a high noi e did no an fe o e o noi e i h hei im li. Thi beha io al ba eline i c i ical beca e i do ble-di ocia e he diffe en ole of do al and en al a ea in di a i oce ing a high and e o noi e le el infe ed f om TMS e l . Ho e e , a imila ba eline ega ding he ecifici / an fe of mo ion di ec ion lea ning f om “noi ” 40% cohe ence o e o-noi e 100% cohe ence i mi ing in Chen e al. (2016). Beca e of i im o ance o he in e e a ion of he TMS da a in Chen e al. (2016), e decided o collec da a fo hi ba eline condi ion.

We had en ne ob e e ac ice mo ion di ec ion lea ning a 40% cohe ence (Fig. 3). T o ob e e ho ed nega i e im- o emen (Fig. 3c, bo om o ob e e) e e e cl ded f om da a 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 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 configuration, the expected baseline of no learning transfer from 40% to 100% coherence, or from noise 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) transferred 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 pre-tests, TMS stimulation were performed and the same pre-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 impact 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 conditions × 2 staircases × 40 trials/staircase), which was sufficient to saturate procedural learning. In Experiment 2, one staircase was practiced for each of two conditions (2 conditions × 1 staircase × 40 trials/staircase = 80 trials). After this initial practice, the pre-tests formally started, and the thresholds 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 impact of possible procedural learning was inconsistent even within these 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 in previous studies (Xiong et al., 2016), when training is performed with the direction threshold measured by a method of same-different comparison with a pair of fixed stimuli, as in earlier studies by Ball and Sekuler (1982, 1987) and Liu (1999), an observer might be able to learn what exactly these local cues to "idiosyncracies" (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 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 we offered in Xiong et al. (2016). Therefore, we felt it necessary to re-test 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 threshold at high noise was ~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 was 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 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 National Science Foundation of China grant 31900799 (XYX). We thank the comments and suggestions from colleagues who also study perceptual learning.

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