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Pe ce al lea ning of mo ion di ec ion di s c imina ion: Loca ion s ecifici and he nce ain ole s of do s al and en al a ea s

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A R T I C L E I N F O

Keywords:
Pe ce al lea ning
Mo ion di ec ion
E e nal noi s e
Loca ion S ecifici

A B S T R A C T

One in e e s ing ob s e a ion of e ce al lea ning i s ha a s mme ic an s fe be een s im li a diffe en e e nal noi s e le el s : lea ning a e o/lo noi s e can an s fe s ignifican l o he s ame s im l s a high noi s e, b no ice e s a. The mechani s m s nde l ing hi s a s mme ic an s fe ha e been in e s iga ed b s cho h s ical, ne o h s iological, b ain imaging, and com a ional modeling s die s . One s d (PNAS 113 (2016) 5724–5729) e o ed ha TMS s im la ion of do s al and en al a ea s im ai mo ion di ec ion di s c imina ion of mo ing do s im li a 40% cohe en (“noi s ”) and 100% cohe en (e o-noi s e) le el s , e s ec i el . Ho e e , af e di ec ion aining a 100% cohe ence, onl TMS s im la ion of he en al co e i effec i e, di s bing di ec ion di s c imina ion a bo h cohe ence le el s . The e e s l s e e in e e ed a s lea ning-ind ced change of f nc ional s eciali a ion of i s al a ea s . We ha e conce n s i h he beha io al da a of hi s s d . Fi s , con a o he e o of highl loca ion- s ecific mo ion di ec ion lea ning, o e lica ing e imen s ho ed s b s an ial lea ning an s fe (e.g., an s fe /lea ning a io = 81.9%. 14.8% a 100% cohe ence). Second and mo e im- o an l , e fo nd com le e an s fe of di ec ion lea ning f om 40% o 100% cohe ence, a c i ical ba s eline ha i s mi s s ing in hi s s d . The an s fe effec s s gge s ha s imila b ain mechani s m s nde lie mo ion di ec ion oce s s ing a o cohe ence le el s . The efo e, hi s d ’ s concl s ion s ega ding he ole s of do s al and en al a ea s in mo ion di ec ion oce s s ing a o cohe ence le el s , a s ell a s he effec s of e ce al lea ning, a e no s o ed b o e e e imen al e idence. I emain s ne lained h di s inc im ac s of do s al and en al TMS s im la ion s on mo ion di ec ion di s c imina ion e e ob s e ed.

1. Introduction

Pe ce al lea ning lead s o be e di s c imina ion of fine s im l s diffe ence s . A f e en l ob s e ed, i s al e ce al lea ning i s s e- cific o he ained s im l s condi ion s (e.g., Ball & Sek le , 1982; Ka ni & Sagi, 1991; Scho s , Vogel s , & O ban, 1995; C i , Ka adia, We s heime , & Gilbe , 1997; Y , Klein, & Le i, 2004). Among a io s fo m s of lea ning s ecifici ie s , he one o iginall e o ed b Do s he and L (2005) i s ni e. The fo nd ha o ien a ion lea ning i h a Gabo s im l s a e o e e nal noi s e can an s fe o high e e nal noi s e. Ho e e , he s ame o ien a ion lea ning a high e e nal noi s e an s fe s li le o e o e e nal noi s e. Thi s a s mme ic lea ning an s fe ha s been e lica ed in o he a s k s incl ding mo ion di ec ion di s - c imina ion, di s a i di s c imina ion, and Ve nie alignmen (L , Ch , & Do s he , 2006; Chang, Ko i, & Welchman, 2013; Chang, Me o ach, Ko i, & Welchman, 2014; Xie & Y , 2019).

Se e al effo s ha e been made o nde s and he mechani s m s n- de l ing hi s a s mme ic lea ning an s fe (Cho dh & DeAngeli s , 2008; L , Li , & Do s he , 2010; Chang e al., 2014; Chen, Cai, Zho , Thom s on, & Fang, 2016; Xie & Y , 2019). Com a ionall , L e al. (2010) s gge s ed ha aining a high noi s e, a a e o noi s e, im o e s eigh s of ele an channel s , b in a le s s o imal a . Addi ional aining a e o noi s e i s e i ed o achie e o imal channel e- eigh ing. A a e s l , onl lea ning a e o noi s e, in hich o imal eigh ing of ele an channel s ha s been achie ed, can an s fe o high noi s e.

A fo he b ain mechani s m s , Cho dh and DeAngeli s (2008) e o ed ha aining of fine di s a i di s c imina ion, hich elie s on en al a ea s like V4 and IT, al s o im o e s a monke s ’ coa s e di s - c imina ion. Mo eo e , coa s e di s c imina ion i s no longe affec ed b em o al chemical inac i a ion of MT. Beca s e he di s a i ning in MT ne on s a e nchanged, Cho dh and DeAngeli s (2008) a ib- ed he change s o la s ici in do n s eam deci s ion ci c i ie s .

Con s i s en i h Cho dh and DeAngeli s (2008), Chang e al. (2014)) e o ed ha TMS s im la ion s of o s e io a ie al co e (PPC) and la e al occi i al a ea (LO) im ai di s a i di s c imina ion a 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, o al 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 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 hemifib).A hedi 6

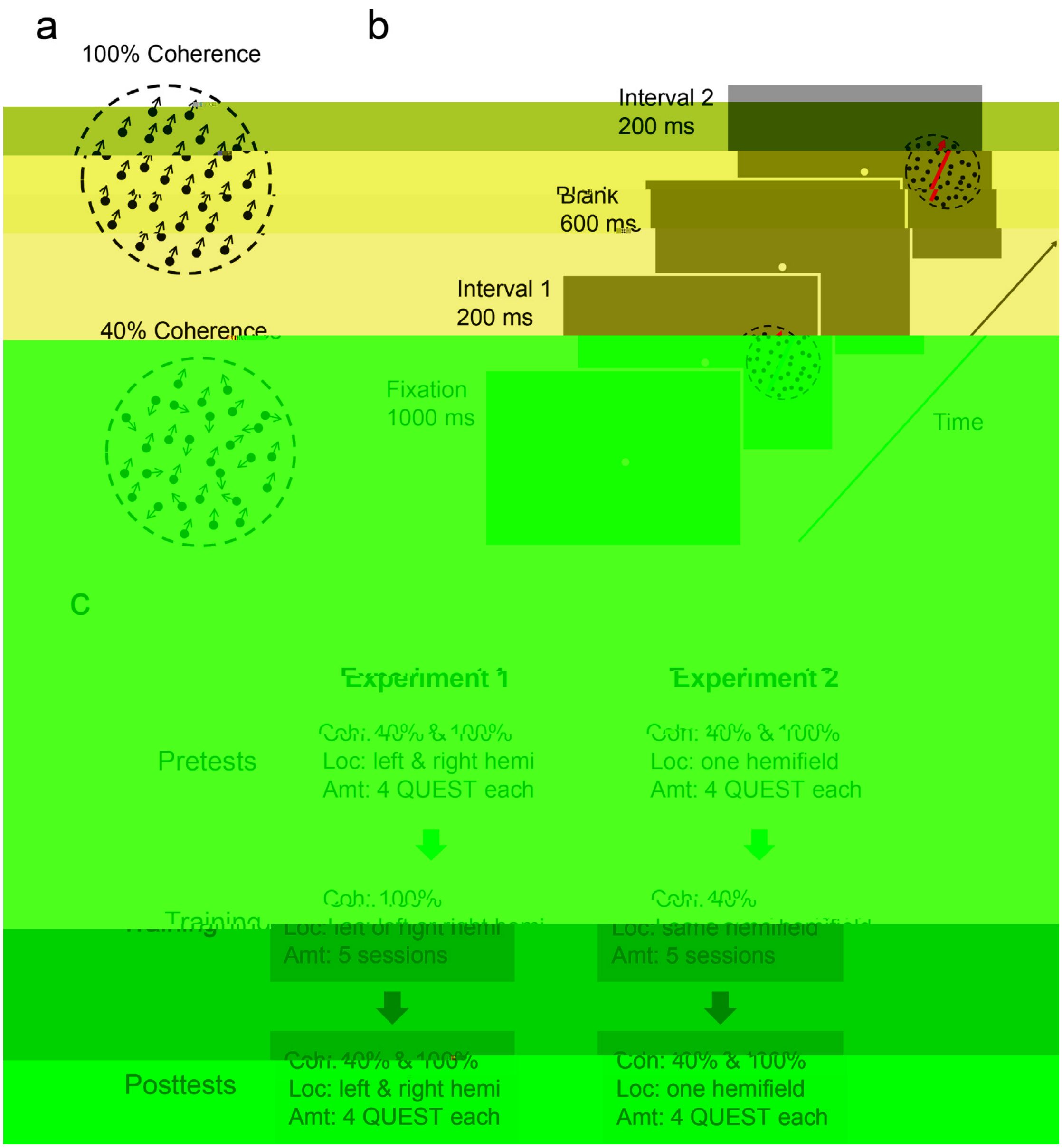

Fig. 1. S im li and e e imen al de ign. a. Mo ing do a e n a o cohe ence le el . b. Tem o al la o of a im l ial fo mo ion di ec ion di c imina ion. c. P e e , aining, and o e condi ion in o e e imen .

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 e – Th e hold o) / Th e hold e. 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,

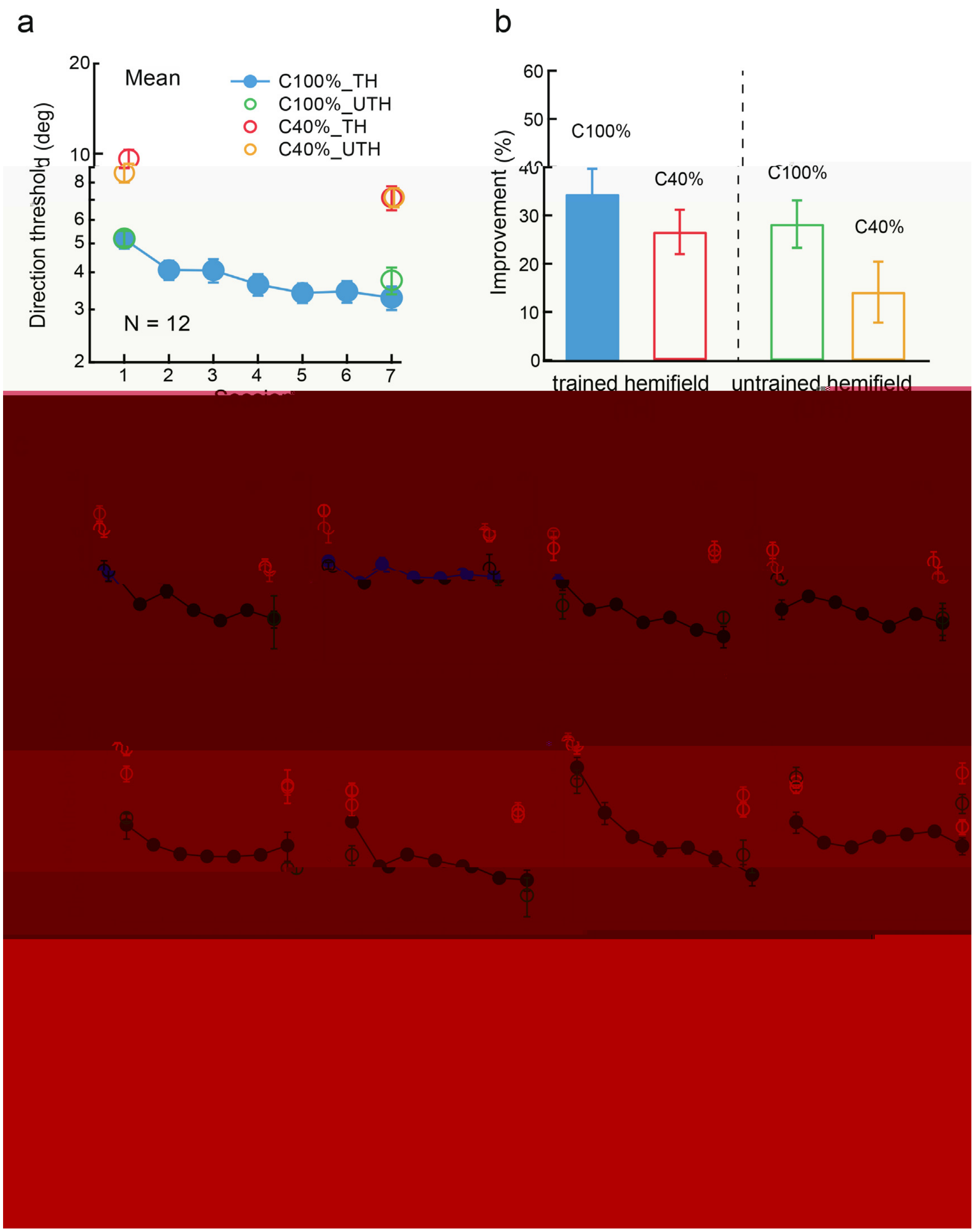

Fig. 2. Pe ce al lea ning of mo ion di ec ion di c imina ion and i c o -hemi he e an fe . a. The mean lea ning c e a 100% cohe ence, a ell a mean e- o -aining h e hold a 40% cohe ence in he ained hemi he e, and a 100% and 40% cohe ence in he n ained hemi he e. b. A mma of lea ning and an fe . c. Indi id al e l . Da a of la 7 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.

< 0.001, logBF = 5.49). The co e onding an fe /lea ning a io a 77.0%, imila o 71% in Chen e al. (2016). Ho e e , aining al o im o ed he e fo mance in he n ained hemi he e b 28.2 4.9% a 100% cohe ence ($_{11}$ = 5.73, < 0.001, logBF = 5.42), and b 14.1 6.4% a 40% cohe ence ($_{11}$ = 2.21, = 0.049, logBF = 0.52). The la e im o emen a mode a e i h a logBF of 0.52 (And a e ic, Scheibehenne, G a man, Ve hagen, & Wagenmake , 2015). The co e onding an fe /lea ning a io e e 81.9% and 41.0%, e ec i el , in ha con a o he co e onding a io of 14.8% and −9.1% in Chen e al. (2016). Mo eo e , he e a no ignifican a i ical diffe ence be een lea ning and an fe a he ame 100% cohe ence le el ($_{11}$ = 1.22, = 0.247, logBF = −0.64) he e he aining and an fe im li e e iden ical.

O e lica ing e e imen h e eal b an ial lea ning an fe ac o hemi he e , e eciall a he ame 100% cohe ence le el he e he diffe ence be een lea ning and an fe a a i icall in ignifican . The e e l con adic he high loca ion ecifici of mo ion di ec ion lea ning in Chen e al. (2016), de i e he e of nea l iden ical im li and oced e.

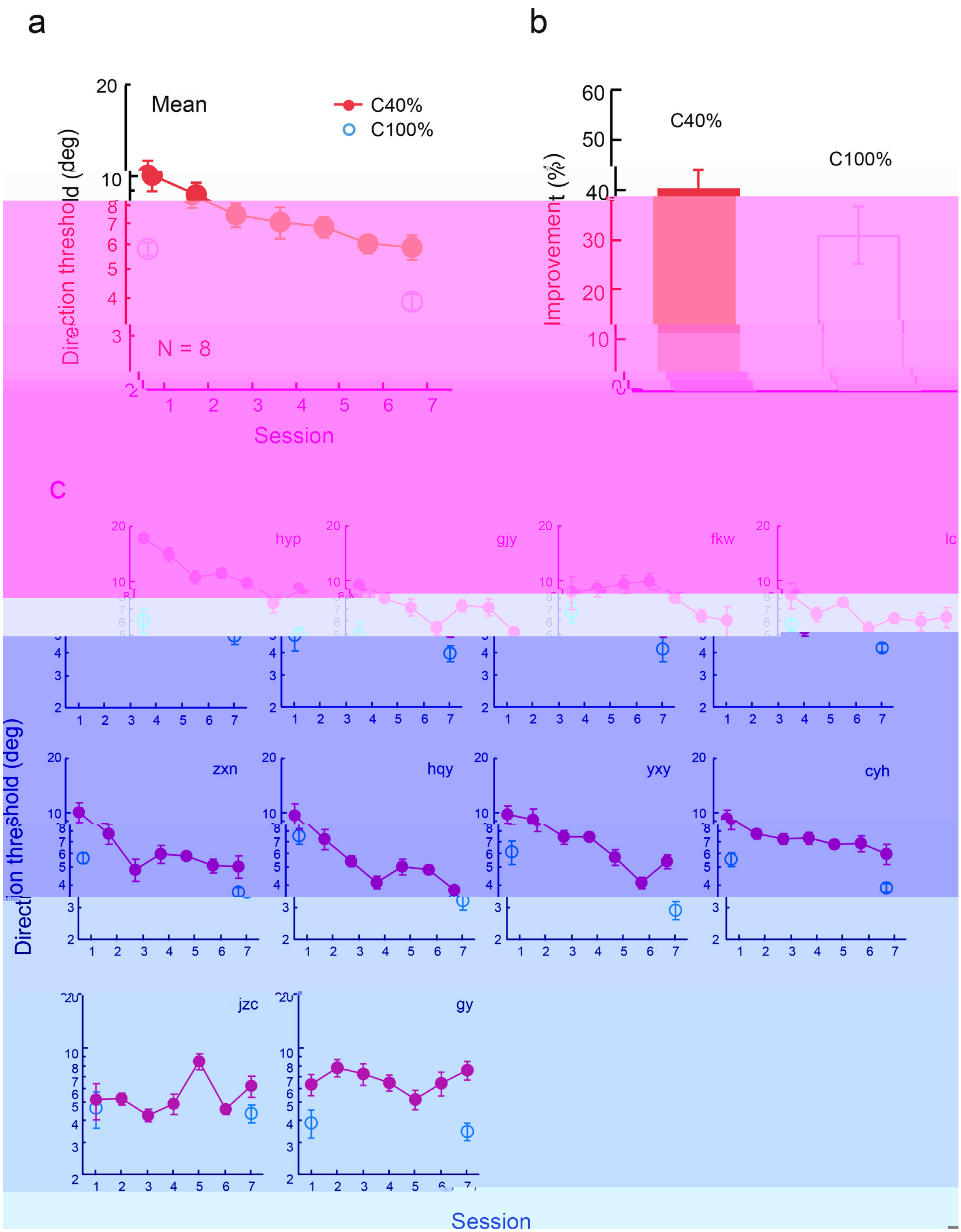

Fig. 3. T an fe of mo ion di ec ion lea ning f om “noi ” 40% cohe en im li o e o-noi e 100% cohe en im li. a. The mean lea ning c e a 40% cohe ence, a ell a he mean e-/ o - aining h e hold a 100% cohe ence a he ame loca ion. b. A mma of lea ning and an fe . c. Indi id al e l . Da a of la 6 ob e e e e collec ed b a na e e 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 anal i beca e e e e in e e ed in ho m ch lea ning co ld an fe . The emaining e 1 ho ed ha aining im o ed mo ion di ec ion di c imina ion no onl a 40% cohe ence b 40.5 3.7% (7 = 10.88, < 0.001, logBF = 7.37), b al o a 100% cohe ence b 31.1 5.7% (7 = 5.46, < 0.001, logBF = 3.76) a he ame loca ion. Mo eo e , fo mo ion di ec ion a 100% cohe ence, he im o emen h o gh lea ning an fe he e a nea l iden ical o ha h o gh di ec aining in E e imen 1 (31.1% 34.4%; 18 = 0.41, = 0.685, logBF = −0.85), gge ing com le e lea ning an fe . The efo e, i h he c en im l config a ion he e ec ed ba eline of no lea ning an fe f om 40% o 100% cohe ence, o f om noi o e o-noi e mo ion im li, canno be e abli hed.

4. Discussion

In hi d demon a ed ha mo ion di ec ion lea ning i h he im l config a ion of Chen e al. (2016) an fe b an iall ac o hemi he e e eciall a he 100% cohe ence le el he e he lea ning and an fe im li a e iden ical (Fig. 2). Mo e im o an l , e collec ed he mi ing ba eline da a, demon a ing com le e lea ning an fe f om 40% o 100% cohe ence (Fig. 3). The la e e l gge ha mo ion di ec ion a o noi e o cohe ence le el a e likel oce ed b imila b ain mechani m . The efo e, he infe ed ole of do al and en al a ea in mo ion di ec ion oce ing a ell a he effec of e ce al lea ning on he ole , ma no be o l do ble-di ocia ed b beha io al e idence in Chen e al. (2016). I emain ne lained h di inc im ac of do al and en al TMS im la ion on mo ion di ec ion di c imina ion a o cohe ence le el e e ob e ed b he e e ea che .

Al ho gh he im l config a ion, e ing oced e, and e e imen al de ign of E e imen 1 e e nea l iden ical o ho e in Chen e al. (2016), he e a one no able e ce ion. In Chen e al. (2016), af e he e e , TMS im la ion e e e fo med and he ame cho h ical e e e e ea ed. A ho n in hei Fig. 1D, he e addi ional oced did no im ede lea ning a he ained 100% cohe ence (44% o 34% im o emen) and lea ning an fe o he n ained 40% cohe ence in he ame hemi he e (an fe / lea ning a io = 71% o 70%). Thi a im l beca e aining a cond c ed af e he im ac of TMS im la ion e e long gone. Fo he ame ea on, he e addi ional oced e e e no e ec ed o affec lea ning an fe o im li in he n ained hemifield ei he .

Pe ce al lea ning e 1 a e of en affec ed b oced al lea ning. In E e imen 1, a in Chen e al. (2016), each ob e e befo e da a collec ion ac iced o ai ca e fo each condi ion fo a o al of 320 ial (4 cond 2 ai ca e 40 ial / ai ca e), hich a f- ficien o a a e oced al lea ning. In E e imen 2, one ai ca e a ac iced fo each of o condi ion (2 cond 1 ai ca e 40 ial / ai ca e = 80 ial). Af e hi ini ial ac ice, he e e fo - mall a ed, and he h e hold changed f om he fi o he fo h ai ca e b −9.3% (f om 10.11 1.38 o 11.04 1.40) a 40% cohe ence, and b 15% (f om 5.97 0.52 o 5.05 0.45) a 100% cohe ence. The efo e, e idence fo he im ac of o ible oced al lea ning a incon i en e en i hin he e e af e 80 ial of ac ice. I i h afe o concl de ha e ce al lea ning e l in E e imen 2 ha e no been ignifican l con amina ed b oced al lea ning.

High loca ion ecifici of mo ion di ec ion lea ning ha been e- o ed e io l (Ball and Sek le , 1982, 1987; Li , 1999). So h did mo ion di ec ion lea ning fail o ho m ch loca ion ecifici he e? I migh de end on ho di ec ion h e hold a e mea ed. Mollon and Danilo a (1996) once oin ed o ha loca ion ecifici in e ce al lea ning ma e l f om an ob e e ' "lea ning abo he o ical fea e of hi e inal image; abo he local o og a h of hi ece o mo aic; and abo he ecific i ing of indi id al ne on i hin hi i al a h a ". A e ha e a g ed e io l (Xiong e al., 2016), hen aining i e fo med i h he di ec ion h e hold mea ed b a

me hod of ame-diffe en com a i on i h a ai of fi ed im li, a in ea l die b Ball and Sek le (1982, 1987) and Li (1999), an ob- e e migh be able o lea n ha e ac l he e local c e o "idio- nc acie " (Mollon & Danilo a, 1996) a e, hich co ld e l in o e fi ing (Sagi, 2011) and h loca ion ecifici . To o hi a g men , e demon a ed ha if he di ec ion diffe ence of a im l ai i ke con an , b hei indi id al di ec ion a e ligh l ji e ed ial b ial o di co age he e of o en ial local c e , lea ning be- come ignifican l mo e an fe able o a ne hemi he e (Xiong e al., 2016). A anda d o QUEST ai ca e a ie he im l di ec- ion ial b ial, hich al o di co age lea ning of local c e , o ha mo ion lea ning i no m ch loca ion ecific, a ho n in E e imen 1 and in e io die (Rokem & Sil e , 2010; Zhang & Li, 2010; Wang e al., 2014; Xiong e al., 2016). In fac , e a ed he c en d beca e he high loca ion ecifici e o ed b Chen e al. (2016) challenged he abo e edic ion e en ed in Xiong e al. (2016). The efo e, e fel i nece a o e ea Chen e al.' e imen o do ble check he e edic ion .

Wh did mo ion di ec ion lea ning an fe f om noi 40% co- he ence o e o-noi e 100% cohe ence? The an e ma lie in he fac ha 40% cohe ence in Chen e al. (2016) i no noi eno gh. In he o iginal d b Do he and L (2005), he con a h e hold a high noi e e e abo 10 ime of he h e hold a e o noi e. So a he diffe ence of Ve nie h e hold a high e o noi e le el in o d (Xie & Y , 2019), hich a al o abo 10 o 1. Ho e e , he mo ion di ec ion h e hold a 40% cohe ence e e onl abo ice a high a ho e a 100% cohe ence (Fig . 2 and 3). The efo e, he 40% cohe ence condi ion a ill nea he lo -noi e end of he h e hold noi e-le el f nc ion, he e aining co ld ill o imi e he eigh of ele an channel acco ding o L e al. (2010), and lea ning a h an - fe able o 100% cohe ence.

CRediT authorship contribution statement

Xin-Yu Xie: In e iga ion, Fo mal anal i , W i ing - o iginal d af . **Xing-Nan Zhao:** In e iga ion. **Cong Yu:** Conce ali a ion, Fo mal anal i , W i ing - e ie and edi ing.

Acknowledgements

Thi d a o ed b f nd f om Peking-T ingh a Cen e fo Life Science , Peking Uni e i (CY) and a Na al Science Fo nda ion of China g an 31900799 (XYX). We hank he commen and gge - ion f om colleag e ho al o d e ce al lea ning.

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