#### **Behavioral/Cognitive**

# **Perceptual Learning at a Conceptual Level**

R Wa ,<sup>1,2\*</sup> J Wa ,<sup>1\*</sup> J -Y Za ,<sup>2\*</sup> X -Y X ,<sup>2\*</sup> Y -Xa Ya ,<sup>2</sup> S -Ha L ,<sup>1</sup> C  $\mathbf{Y}_{1}$ ,<sup>2</sup> a d W. L<sup>1</sup> 1State Key Laboratory of Cognitive Neuroscience and Learning and IDG/McGovern Institute for Brain Research, Beijing Normal University, Beijing 100875, China, and <sup>2</sup>Department of Psychology, IDG/McGovern Institute for Brain Research, and Peking-Tsinghua Center for Life Sciences, Peking University 100871 Beijing, China

Humans can learn to abstract and conceptualize the shared visual features defining an object category in object learning. Therefore, learning is generalizable to transformations of familiar objects and even to new objects that differ in other physical properties. In contrast, visual perceptual learning (VPL), improvement in discriminating fine differences of a basic visual feature through training, is commonly regarded as specific and low-level learning because the improvement often disappears when the trained stimulus is simply relocated or rotated in the visual field. Such location and orientation specificity is taken as evidence for neural plasticity in primary visual cortex (V1) or improved readout of V1 signals. However, new training methods have shown complete VPL transfer across stimulus locations and orientations, suggesting the involvement of high-level cognitive processes. Here we report that VPL bears similar properties of object learning. Specifically, we found that orientation discrimination learning is completely transferrable between luminance gratings initially encoded in V1 and bilaterally symmetric dot patterns encoded in higher visual cortex. Similarly, motion direction discrimination learning is transferable between first- and second-order motion signals. These results suggest that VPL can take place at a conceptual level and generalize to stimuli with different physical properties. Our findings thus reconcile perceptual and object learning into a unified framework.

Key words: perceptual learning; motion direction; orientation; transfer

#### ca c S.a.

Training in object recognition can produce a learning effect that is applicable to new viewing conditions or even to new objects with different physical properties. However, perceptual learning has long been regarded as a low-level form of learning because of its specificity to the trained stimulus conditions. Here we demonstrate with new training tactics that visual perceptual learning is completely transferrable between distinct physical stimuli. This finding indicates that perceptual learning also operates at a conceptual level in a stimulus-invariant manner.

#### I \_\_\_\_ d c

S

O, .			a a	a				а,		a a	
. a		а							2	<b>1</b> , 7	a
	. S .			:	a .	а.,	. , .	,	a		, a, /
a	a				J	,	a	а	a		
·· .	. ,		а	a			J	a		(B	a.,

Received July 19, 2015; revised Dec. 10, 2015; accepted Jan. 9, 2016.

Author contributions: J.-Y.Z., C.Y., and W.L. designed research; R.W., J.W., X.-Y.X., Y.-X.Y., and S.-H.L. performed research; R.W., J.W., J.-Y.Z., X.-Y.X., C.Y., and W.L. analyzed data; C.Y. and W.L. wrote the paper.

This work was supported by National Key Basic Research Program of China (Grant 2014CB846101) and the National Natural Science Foundation of China (Grants 31230030, 31470975, and 91432102). We thank Gerald Westheimer and Rufin Vogels for valuable comments.

The authors declare no competing financial interests

\*R.W., J.W., J.-Y.Z., and X.-Y.X. contributed equally to this work.

Correspondence should be addressed to either of the following: Cong Yu, Department of Psychology, Peking University, Beijing 100871, China, E-mail: yucong@pku.edu.cn; or Wu Li, State Key Laboratory of Cognitive Neuroscience and Learning, Beijing Normal University, Beijing 100875, China, E-mail: liwu@bnu.edu.cn. DOI:10.1523/JNEUROSCI.2732-15.2016

Copyright © 2016 the authors 0270-6474/16/362238-09\$15.00/0

1956; R . . . . a . . Ra , 2006). A a ..., а J . , , , , , , , , , , , , , , a . . S , a а а a a, a a J . . . . . . . . . . / . . C . . . . а ., , а , , , а . . , а , . . . , а , а . . . , . . a. , a , a а а , a., (Fa 2002). F . , . . . . ) . a . . . ' . . . a . а ..., ...., .a..., .a., , . a a a a a , , , , a, . a. a a . a , a , . . . . . . . . a

..., a., a., (Ka., a., Sa., 1991; S., ... . a. Da. a, 1996; D. . . a. L., 1999; La a. (M G , 2009).

(X a \_ a ., 2008; J.Y.Z a \_ a ., 2010; Z a \_ a / Ya , a , . . , a, . . , . a . . . a a a . . . a a . a a version a version of the VPL. , a

. a. . . ., . **.** I ... a. ... . ,. ,. ,. . a... . . , . . . a . . . , . . . . , a . . , a . . . , a, ..., ..., a VPL a, a ..., a ..., a ..., a a j a l j a l j ..., . ... a v j a a VPL a ...a , a, / , / , / , , , a , .

### Ma a d M d

×768 ,0.38 × 0.38 , 120 H a a ). T a a  $a = 50 / a^2$ . T a a  $a = a^2$ . a  $a = -a^2$ . V a  $a = -a^2$ . A  $a = -a^2$ . 

a (F.5F). Visual stimuli. T 

SD
Ga
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a
a a .

a . . . . . . . . a

a -

Experimental procedure. I \_\_\_\_\_a \_\_\_, . , . . 

a. / . a, a 



Figure 1. Transfer of orientation discrimination learning from symmetric dot patterns to gratings. A, Sample stimuli. The symmetry axis is indicated by the red dashed line (not shown in the actual stimuli). The arrow indicates the direction of learning transfer. B, Session-by-session mean discrimination thresholds for dot pattern orientation ("Dots") and grating orientation ("Gabor" or "Noise"). Grating orientation discrimination was tested with Gabor gratings (left) and noise gratings (right). C, Summary of dot pattern orientation learning and its transfer to grating orientation ("Training]" and "Transfer"; left two bars) and the impact of further grating orientation training ("Training2"; right bar). Data are averaged over the two panels in **B**. The percentage improvement was calculated as (pretraining threshold - posttraining threshold)/pretraining threshold. Error bars indicate  $\pm$  SEM.

W , а. . .

## R . . . .

,..., a ..., a ..., a... ...., T, ...., ...., a..., a... a a -a a a.T. (H a, W, , 1959, 1962), , a a . . a . . -a -a ., 2005; T a ., 2005). T a., aGa a...., ), , , , a , , ... V1 (Wa a., 1983). B a , a a a a Ga a a а a., 1995). . . . . -Т a . T a , , , a, , W a a a., ,.,.. ... a . , ... a .

, a 125 ( . . . . . a a . . . . a . ).F

)  $(35.1 \pm 3.4\%, p < 0.001, C$ , d = 2.78; F, 1B,C). T (.a.) ... a a / ... a, ... (p = 0.12, C, ..., d = 0.44), ..., a ..., a. ..., a. ..., a. , . . a. . . . .

a (5.4 ± 3.5%, p = 0.15, C , . . ' d = 0.41; F . 1*B*, *C*), / . . . , a / . . . a a a . . . a a a 

a 35 125, a a  $40.1 \pm$ 



 


 $(36.8 \pm 4.9\%, p = 0.001, C, ..., d = 3.0). A$ a, a, a, a, a,  $(5.3 \pm 3.7\%, p = 0.22, C$ , aa., , . a. . . . , . . - . . . . . . . . 0.001, C , a a (18.3  $\pm$  4.3%, p = 0.008, C (17.6). T  $22.0 \pm$  $40.3 \pm 4.0\%$ . T .a.,  $(-0.2 \pm 6.0\%, p = 0.75, C, ..., d = -0.15),$  a , a \_  $(-1.1 \pm 2.5\%, p = 0.45, C, d = -0.20)$ . T a . / ... . **a** . . , . . . . . . **. a** . . . a -. . **a** . , . . . . . **a** . . . . , . .a, ). W. a. a., .a, . j, , ...a. .a j...a. a, ..., .a, ..., a. .N. ...a a 1.82). To a a a sola a sola a sola PSE of a sola a sola PSE of a sola a so ν...., τΡΕ (F. . 5*C*). Τ, τ. ...., α..., α...,

## D

a а 2015). M ...., MRI .... a a a a . a a a -aa. P...., a. ..., a. Ha , 2010; Va , a a. C. , 2012

Matthews N, Liu Z, Geesaman BJ, Qian N (1999) Perceptual learning dWang R, Zhang JY, Klein SA, Levi DM, Yu C (2014) Vernier perceorientation and direction discrimination. Vision Res 39:3692-3701. ptual learning transfers to completely untrained retinal locations CrossRef Medline after double training: a "piggybacking" effect. J Vis 1402bssRef

Moldakarimov S, Bazhenov M, and Sejnowski TJ (2014) Top-down inputs Medline enhance orientation selectivity in neurons of the primary visual cortexWatson AB, Barlow HB, Robson JG (1983) What does the eye see best? during perceptual learning. PLoS Comput Bio 10(8), e10032700ssRef

- Spat Vis 10:51-5& rossRef Medline
- Pelli DG (1997) The VideoToolbox software for visual psychophysics: transforming numbers into movies. Spat Vis 10:437-4020ssRef Medline
- Petrov AA, Hayes TR (2010) Asymmetric transfer of perceptual learning of luminance- and contrast-modulated motion. J Vis 10: Medline
- Ramalingam N, McManus JN, Li W, Gilbert CD (2013) Top-down modulation of lateral interactions in visual cortex. J Neurosci 33:1773-1789.
- of categorization. Curr Dir Psychol Sci 15:9-CBossRef
- Sasaki Y, Vanduffel W, Knutsen T, Tyler C, Tootell R (2005) Symmetry an Y, Rasch MJ, Chen M, Xiang X, Huang M, Wu S, Li W (2014) Percepactivates extrastriate visual cortex in human and nonhuman primates. Proc Natl Acad Sci U S A 102:3159-3160ossRef Medline
- Schoups AA, Vogels R, Orban GA (1995) Human perceptual learning in Schoups AA, Vogels R, Orban GA (1995) Human perceptual learning in Enclosed and the school of the schoo and monocularity. J Physiol 483:797-8000ssRef Medline

Shiu LP, Pashler H (1992) Improvement in line orientation discrimination is retinally local but dependent on cognitive set. Percept Psychophys 52 hang JY, Yang YX (2014) Perceptual learning of motion direction discrim-582–588CrossRef Medline

- 582–586 Joss Rei Medime Teich AF, Qian N (2003) Learning and adaptation in a recurrent model of Shang JY, Zhang GL, Xiao LQ, Klein SA, Levi DM, Yu C (2010a) Rule-based Zhang JY, Zhang GL, Xiao LQ, Klein SA, Levi DM, Yu C (2010a) Rule-based
- Tyler CW, Baseler HA, Kontsevich LL, Likova LT, Wade AR, Wandell BA (2005) Predominantly extra-retinotopic cortical response to pattern symmetry. Neuroimage 24:306-3C4ossRef Medline
- Vaina LM, Chubb C (2012) Dissociation of first- and second-order motion systems by perceptual learning. Atten Percept Psychophys 74:1009–1019 sation. Invest Ophthalmol Vis Sci 55:2020–2030 as Ref Medline CrossRef Medline
- Vogels R, Orban GA (1987) Illusory contour orientation discrimination. Vision Res 27:453-462 rossRef Medline
- demand modulate double-training enabled transfer of perceptual learning. Vision Res 61:33-38 rossRef Medline

Nature 302:419-422 rossRef Medline Mollon JD, Danilova MV (1996) Three remarks on perceptual learning Wörgötter F, Eysel UT (1991) Axial responses in visual cortical cells: spatio-

temporal mechanisms quantified by Fourier components of cortical tuning curves. Exp Brain Res 83:656-6664dline Xiao LQ, Zhang JY, Wang R, Klein SA, Levi DM, Yu C (2008) Complete

- transfer of perceptual learning across retinal locations enabled by double training. Curr Biol 18:1922-1926 rossRef Medline
- Xiong YZ, Zhang JY, Yu C (2015) Under-stimulation at untrained orientation may explain orientation specificity in perceptual learning. J Vis 15:38. CrossRef Medline

Rouder JN, Ratcliff R (2006) Comparing exemplar- and rule-based theories direction learning associated with training with a single-level method of constant stimuli. Vision Res 119:9-CrossRef Medline

tual training continuously refines neuronal population codes in primary

by retinotopic processing and attentional remapping. Eur J Neurosci 38: 3758-3767CrossRef Medline

ination transfers to an opposite direction with TPE training. Vision Res

learning explains visual perceptual learning and its specificity and transfer. J Neurosci 30:12323-12328ossRef Medline

Zhang JY, Cong LJ, Klein SA, Levi DM, Yu C (2014) Perceptual learning improves adult amblyopic vision through rule-based cognitive compen-

- Zhang T, Xiao LQ, Klein SA, Levi DM, Yu C (2010b) Decoupling location specificity from perceptual learning of orientation discrimination. Vision Res 50:368-37 Gross Ref Medline
- Wang R, Zhang JY, Klein SA, Levi DM, Yu C (2012) Task relevancy an Zhang GL, Cong LJ, Song Y, Yu C (2013b) ERP P1-N1 changes associated with Vernier perceptual learning and its location specificity and transfer. J Vis 13:19Medline