

# Rule-Based Learning Explains Visual Perceptual Learning and Its Specificity and Transfer

Jun-Yun Zhang,<sup>1</sup> Gong-Liang Zhang,<sup>1</sup> Lu-Qi Xiao,<sup>1</sup> Stanley A. Klein,<sup>2</sup> Dennis M. Levi,<sup>2</sup> and Cong Yu<sup>1</sup>

<sup>1</sup>State Key Laboratory of Cognitive Neuroscience and Learning, Beijing Normal University, Beijing 100875, China, and <sup>2</sup>School of Optometry and Helen Wills Neuroscience Institute, University of California, Berkeley, California 94720

Visual perceptual learning models, as constrained by orientation and location specificities, propose that learning either reflects changes in V1 neuronal tuning or reweighting specific V1 inputs in either the visual cortex or higher areas. Here we demonstrate that, with a training-plus-exposure procedure, in which observers are trained at one orientation and either simultaneously or subsequently passively exposed to a second transfer orientation, perceptual learning can completely transfer to the second orientation in tasks known to be orientation-specific. However, transfer fails if exposure precedes the training. These results challenge the existing specific perceptual learning models by suggesting a more general perceptual learning process. We propose a rule-based learning model to explain perceptual learning and its specificity and transfer. In this model, a decision unit in high-level brain areas learns the rules of reweighting the V1 inputs through training. However, these rules cannot be applied to a new orientation/location because the decision unit cannot functionally connect to the new V1 inputs that are unattended or even suppressed after training at a different orientation/location, which leads to specificity. Repeated orientation exposure or location training reactivates these inputs to establish the functional connections and enable the transfer of learning.

## Introduction

Visual perceptual learning (VPL) is a form of learning that occurs when observers are repeatedly exposed to a task that requires them to discriminate between stimuli that differ in a specific feature (Karni and Sagi, 1991; Fahle, 1994; Ahissar et al., 1997), leading to improvements in performance over time. VPL has been extensively studied in the context of orientation discrimination (Ahissar et al., 1997; Fahle, 1994; Zhang et al., 2003; Zenger and Fahle, 2003) and location discrimination (Petrov et al., 1992; Doherty and Lomber, 1998). A rule-based learning model (Marr and Sagi, 1996) has been proposed to explain VPL, suggesting that learning occurs through the reweighting of V1 inputs. This model has been used to explain the specificity and transfer of VPL (Liu and Greenlee, 2009). However, this model has been challenged by recent findings (Xiang et al., 2008). First, it has been shown that VPL can occur even when the training and transfer orientations are different (Marr and Sagi, 1996). Second, it has been shown that VPL can occur even when the training and transfer locations are different (Riesenhuber and Poggio, 1997). Third, it has been shown that VPL can occur even when the training and transfer tasks are different (Touge et al., 2008). These findings challenge the rule-based learning model and suggest that VPL may be a more general form of learning.

Here we demonstrate that, with a training-plus-exposure procedure, in which observers are trained at one orientation and either simultaneously or subsequently passively exposed to a second transfer orientation, perceptual learning can completely transfer to the second orientation in tasks known to be orientation-specific. However, transfer fails if exposure precedes the training. These results challenge the existing specific perceptual learning models by suggesting a more general perceptual learning process. We propose a rule-based learning model to explain perceptual learning and its specificity and transfer. In this model, a decision unit in high-level brain areas learns the rules of reweighting the V1 inputs through training. However, these rules cannot be applied to a new orientation/location because the decision unit cannot functionally connect to the new V1 inputs that are unattended or even suppressed after training at a different orientation/location, which leads to specificity. Repeated orientation exposure or location training reactivates these inputs to establish the functional connections and enable the transfer of learning.

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Correspondence should be addressed to Cong Yu, State Key Laboratory of Cognitive Neuroscience and Learning, Beijing Normal University, Beijing 100875, China. E-mail: yucong@bnu.edu.cn.

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## Materials and Methods

**Observers and apparatus.** Five observers (A, B, C, D, E) participated in the experiment. They were all right-handed and had normal or corrected-to-normal vision. The experiment was conducted using a personal computer (Dell) running MATLAB (The MathWorks, Natick, MA) and Psychtoolbox (Brain Research Laboratories, University of California, Berkeley, CA). The stimuli were presented on a 21-inch monitor (1440 × 900 pixels) at a viewing distance of 57 cm. The background was black, and the stimuli were white.

T. I. G. (1024 × 768; 0.37 × 0.37; 120 Hz; 50 / 2). L. A. E. (1024 × 768; 0.37 × 0.37; 150 Hz; 41 / 2). L. A. E. (8-). A. V.

**Stimuli.** T. G. (G. = 6, SD = 0.17, t = 0.47, (F. 1a), (F. 1, 2). T. ( = 17). T.

T. (F. 3a). A. H. (1997). S. 7 × 7 (22.2 × 1.3). 42.5 ± 3.9. 2. T. (F. 3a), 16. T. (SOA), 7 × 7. 90.

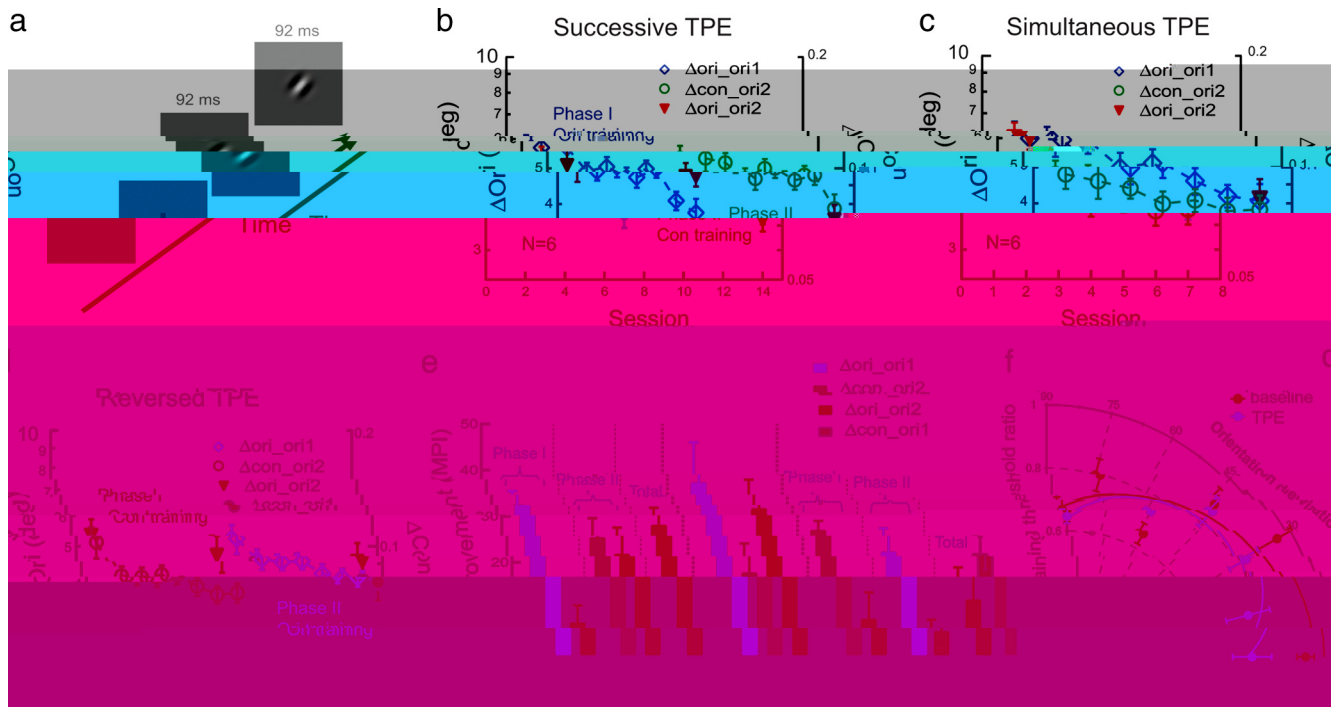
**Procedure.** C. (2AFC) I. + Δ. Δ. (92. 600. T. (200). T. 200. T. / E. I. (6.7). SOA. T. (50% t.). A.

T. 79.4%. T. 0.05. E. T.

## Results

### Orientation specificity and transfer in orientation learning

W. S. (W. ?) G. (F. 1a) (36 / 126, Δ = 1, 1). A. 2,



**Figure 1.** Perceptual learning of orientation discrimination and its transfer to a second orientation studied with TPE procedures. **a**, The stimulus configuration for orientation discrimination in which one interval contained a more clockwise Gabor stimulus. **b**, Successive TPE procedure. Phase I (sessions 1–7): orientation discrimination was practiced at one orientation ( $36^\circ/126^\circ$ ,  $\Delta\text{ori\_ori1}$ , blue diamonds); orientation thresholds indicated by the left ordinate and the transfer of learning was tested at an untrained orthogonal orientation ( $126^\circ/36^\circ$ ,  $\Delta\text{ori\_ori2}$ , the left two red triangles), which replicated typical orientation specificity in orientation discrimination learning. Phase II (sessions 8–14): the same observers were later exposed to the transfer orientation ori2 in a contrast-discrimination learning task around the same transfer orientation ( $126^\circ/36^\circ$ ,  $\Delta\text{con\_ori2}$ , green circles; contrast thresholds indicated by the right ordinate) and the transfer of orientation learning to ori2 was reexamined ( $126^\circ/36^\circ$ ,  $\Delta\text{ori\_ori2}$ , the right two red triangles). Thresholds are averaged over all observers' data; error bars represent one SEM. The left and right ordinates have the same scale factor in log units. **c**, Simultaneous TPE procedure: orientation discrimination was practiced at ori1 ( $\Delta\text{ori\_ori1}$ , blue diamonds) while the transfer orientation ori2 was exposed in a contrast-discrimination learning task ( $\Delta\text{con\_ori2}$ , green circles) and the transfer of learning was tested for orientation discrimination at ori2 ( $\Delta\text{ori\_ori2}$ ; red triangles). **d**, Reversed TPE procedure. Phase I (sessions 1–7): contrast discrimination was practiced around ori2 ( $\Delta\text{con\_ori2}$ ; open green circles) and the change of orientation discrimination performance was measured at ori2 ( $\Delta\text{ori\_ori2}$ ; left two red triangles). Phase II (sessions 8–14): orientation discrimination was practiced at ori1 ( $\Delta\text{ori\_ori1}$ ; blue diamonds) and the transfer of learning was measured at ori2 ( $\Delta\text{ori\_ori2}$ ; right two red triangles). The untrained contrast threshold at ori1 ( $\Delta\text{con\_ori1}$ ) was also measured after the TPE procedure (solid green circle with black outline). **e**, A summary of learning and transfer. Left, Successive TPE in **b**; middle, simultaneous TPE in **c**; right, reversed TPE in **d**. **f**, The average posttraining/pretraining threshold ratios at various orientation deviations from the transfer orientations ( $36^\circ/126^\circ$ ) with conventional (red circles, fitted with a Gaussian peaked at  $0^\circ$  orientation deviation) and TPE training (blue circles, fitted with the difference of two identical Gaussians peaked at  $0^\circ$  and  $90^\circ$  orientation deviations).

... ( $\Delta\text{ori\_ori2}$ ;  $t_{(7)} = 10.1$ ,  $p < 0.001$ ). G...  
 ... (MPI =  $26.9 \pm 2.1\%$ ,  $p < 0.001$ ) (Fig. 1d,e), ...  
 ... ( $\Delta\text{ori\_ori2}$ ; MPI =  $7.7 \pm 5.8\%$ ,  $p = 0.083$ ).

In the successive TPE procedure (Fig. 1b), ...  
 ... ( $\Delta\text{ori\_ori1}$ ; MPI =  $22.2 \pm 5.1\%$ ,  $p = 0.004$ ) (Fig. 1d,e). However, ...  
 ... ( $\Delta\text{ori\_ori2}$  (MPI =  $5.0 \pm 2.6\%$ ,  $p = 0.053$ ) (Fig. 1d,e). Thus, ...  
 ... (Fig. 1e, W).

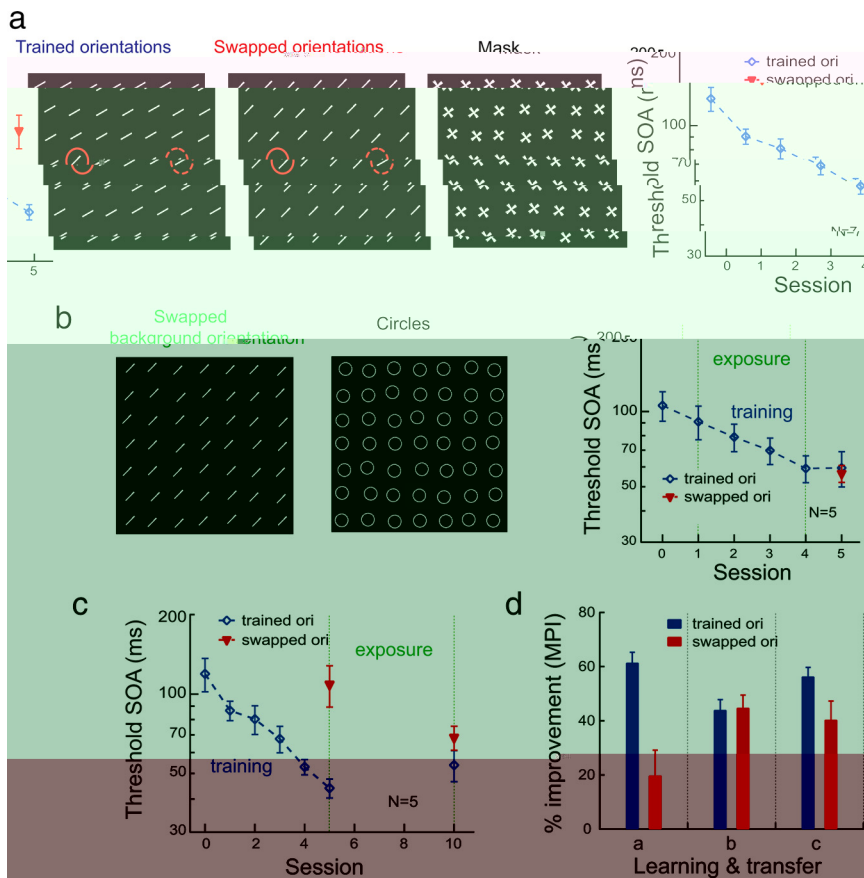
Reversed TPE procedure (Fig. 1d), ...  
 ... ( $\Delta\text{ori\_ori1}$ ; MPI =  $22.6 \pm 3.6\%$ ,  $p = 0.001$ ) (Fig. 1d, ...  
 ... ( $\Delta\text{ori\_ori2}$  ( $p = 0.13$ ), ...  
 ... H... TPE...  
 ... TPE...  
 ... T...

... TPE... H...  
 ...  $\Delta\text{ori\_ori1}$ ... TPE...  
 ...  $\Delta\text{ori\_ori2}$ ...  
 ...  $\Delta\text{ori\_ori1}$ , T... F... 2...  
 W...  
 TPE... F...  
 TPE...  
 ... 0, 15, 30, 45, ... 60...  
 ... ( $36^\circ/126^\circ$ )...  
 T...  
 ... 2. A...  
 ...  
 W...  
 TPE...  
 (F... 1f). B... 30...  
 TPE...

### Orientation specificity and transfer in contrast learning

The TPE... (Fig. 2). T... (Δ... 1; MPI = 29.1 ± 4.1%,  $p < 0.001$ ) (Fig. 2*b,e*). T... (Δ... 2; MPI = 11.6 ± 3.0%,  $p = 0.006$ ), ... (Δ... 1 ( $p = 0.020$ ).

A TPE... (Δ... 1), ... (Δ... 2, ...). H... 2, ... A... 2, ... 1. T... G... (0... 30% to 67%, ±1... 0.47...)



**Figure 3.** The effect of TPE training on transfer of feature detection learning across orientations. *a*, Left three panels, Stimuli at trained target-distracter orientations ( $46^\circ$  vs  $30^\circ$ ), at untrained target-distracter swapped orientations ( $30^\circ$  vs  $46^\circ$ ), and the mask. The odd element (target) could appear at one of two positions (indicated by red circles that were not present in the actual stimuli). Right, Feature detection was practiced at trained target-distracter orientations (blue diamonds) and the transfer of learning was tested at swapped orientations (red triangles). The mean threshold over the first six staircase runs was taken as the baseline and is indicated by the 0th session. *b*, Left and middle, Uniform stimulus array containing swapped-background orientation only or containing circles for the bars or circles judgment (the exposure condition). Right, Feature detection was practiced at trained target-distracter orientations (blue diamonds) and the swapped background orientation was repeatedly exposed (bars or circles) in alternating blocks of trials. The transfer of learning was tested at swapped orientations (red triangles). *c*, The effects of later repeated exposure to the swapped-background orientation after baseline training in five observers from *a*, *d*. A summary of learning and transfer. Left, Baseline training in *a*; middle, simultaneous TPE training in *b*; right, successive TPE training in *c*, in which the performance improvement was calculated by comparing the thresholds at the final 10th session and the 0th session.

(Fig. 3a, Table 1). A... H... (1997)... MPI = 61.4 ± 3.9%,  $p < 0.001$ ,... (MPI = 19.7 ± 9.5%,  $p = 0.041$ ) (E...

33.9 ± 5.3% ( $p = 0.002$ )... (10%)... MPI = 56.2 ± 3.4% ( $p < 0.001$ )... 40.3 ± 7.0% ( $p = 0.004$ )... ( $p = 0.12$ ).

**Discussion**  
**Existing models of perceptual learning predicting specificity, not transfer**  
 T... (Fig. 1, 3)... (X... 2008; Z... 2010)... F... V1-... (A... 2002; T... Q... 2003; Z... 2003)... -V1... (P... 1992; D... L... 1998). T... S...

(Miyamoto and Doherty, 1996; Luo and Gauthier, 2009). A similar pattern of learning was observed in the TPE (Fig. 3). The learning curve in the TPE (Fig. 3) is similar to that in the FPE (Fig. 1b), suggesting that the learning mechanism in the TPE is similar to that in the FPE (Doherty and Luo, 2007). The learning curve in the FPE (Fig. 1b, 3c) is similar to that in the TPE (Fig. 3), suggesting that the learning mechanism in the FPE is similar to that in the TPE (Doherty and Luo, 2007). The learning curve in the FPE (Fig. 1b, 3c) is similar to that in the TPE (Fig. 3), suggesting that the learning mechanism in the FPE is similar to that in the TPE (Doherty and Luo, 2007).

**A rule-based learning model**

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*Rule-based learning*

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*Rule application: specificity and transfer*

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