

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

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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) models (Karni and Sagi, 1991; Fahle, 1994; Ahissar and Hochstein, 1997), which propose that learning reflects changes in V1 neuronal tuning or reweighting specific V1 inputs in either the visual cortex or higher areas, have been widely used to explain VPL. 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.

(Ling and Greenlee, 2009). 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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## Materials and Methods

**Observers and apparatus.** Five observers (A, B, C, D, and E) participated in the experiment. They were all right-handed and had normal or corrected-to-normal vision. The experiment was conducted in a dimly lit room. The stimuli were presented on a computer monitor. The distance between the observer and the monitor was 57 cm. The monitor was 45 cm wide and 30 cm high. The resolution was 1024 × 768 pixels. The refresh rate was 60 Hz. The background was black. The stimuli were white. The contrast was 100%. The size of the stimuli was 1.5° × 1.5°. The orientation was 45°. The location was 1.5° from the center. The training and transfer orientations were 45° and 135°. The training and transfer locations were 1.5° and 4.5° from the center. The training and transfer durations were 10 and 20 trials. The training and transfer intervals were 10 and 20 trials. The training and transfer blocks were 10 and 20 trials. The training and transfer sessions were 10 and 20 trials. The training and transfer days were 10 and 20 days. The training and transfer weeks were 10 and 20 weeks. The training and transfer months were 10 and 20 months. The training and transfer years were 10 and 20 years.

T<sub>1</sub> (N = 21). G (1024 × 768; 0.37 × 0.37; 120 Hz; 50 /s<sup>2</sup>). L (21; D P1130; 1024 × 768; 0.37 × 0.37; 150 Hz; 41 /s<sup>2</sup>). A (8; V).

**Stimuli.** T<sub>1</sub> (G) = 6, SD = 0.17, t = 0.47, (F<sub>(1,2)</sub>) = 17. T<sub>2</sub> (G) = 4, SD = 0.17, t = 0.47, (F<sub>(1,2)</sub>) = 17.

T<sub>1</sub> (F<sub>(1,3a)</sub>) = 2. T<sub>2</sub> (F<sub>(1,3a)</sub>) = 16. T<sub>1</sub> (SOA) = 7 × 7 = 49. T<sub>2</sub> (SOA) = 7 × 7 = 49.

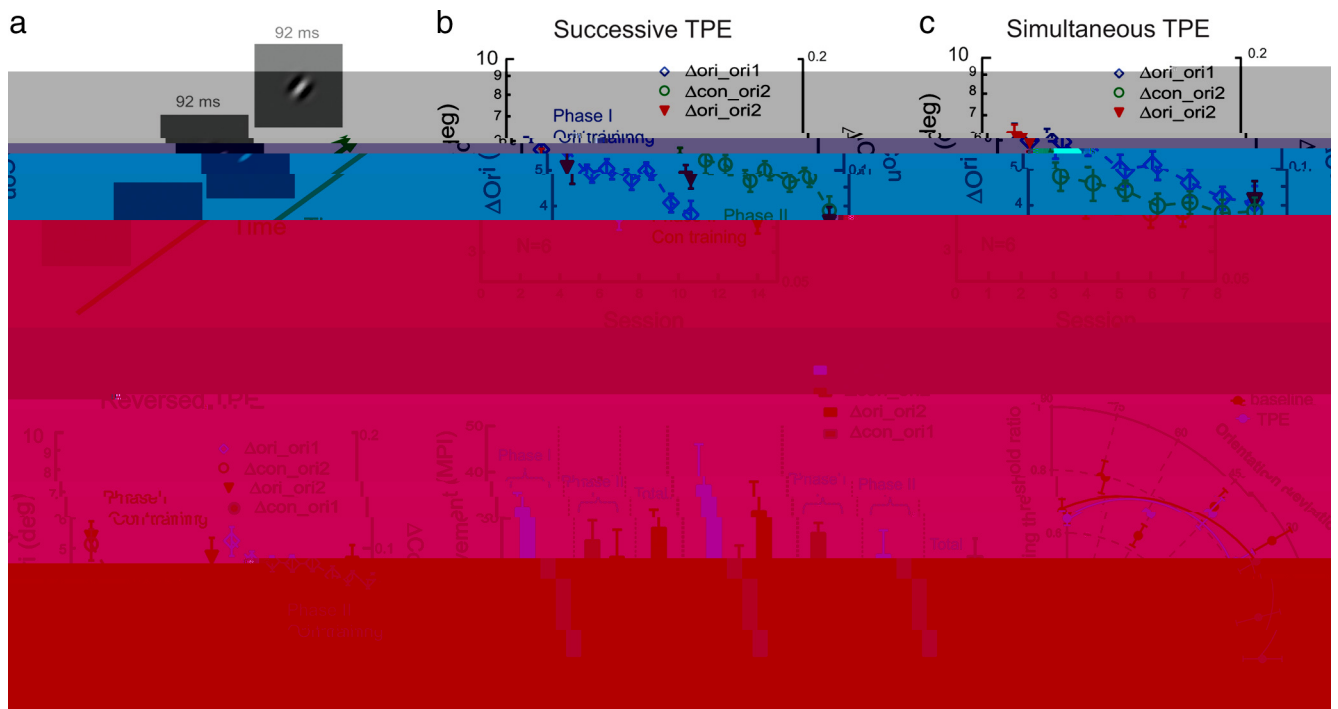
**Procedure.** C (2AFC) (Δ + Δ) (92). T<sub>1</sub> (600). T<sub>2</sub> (200). T<sub>1</sub> (200). T<sub>2</sub> (200). T<sub>1</sub> (6.7). T<sub>2</sub> (6.7). T<sub>1</sub> (50%). T<sub>2</sub> (50%).

T<sub>1</sub> (79.4%). T<sub>2</sub> (0.05). T<sub>1</sub> (0.05). T<sub>2</sub> (0.05).

## Results

### Orientation specificity and transfer in orientation learning

W (S) (W) (G) (F<sub>(1,1a)</sub>) (36) (Δ = 1). A (2).



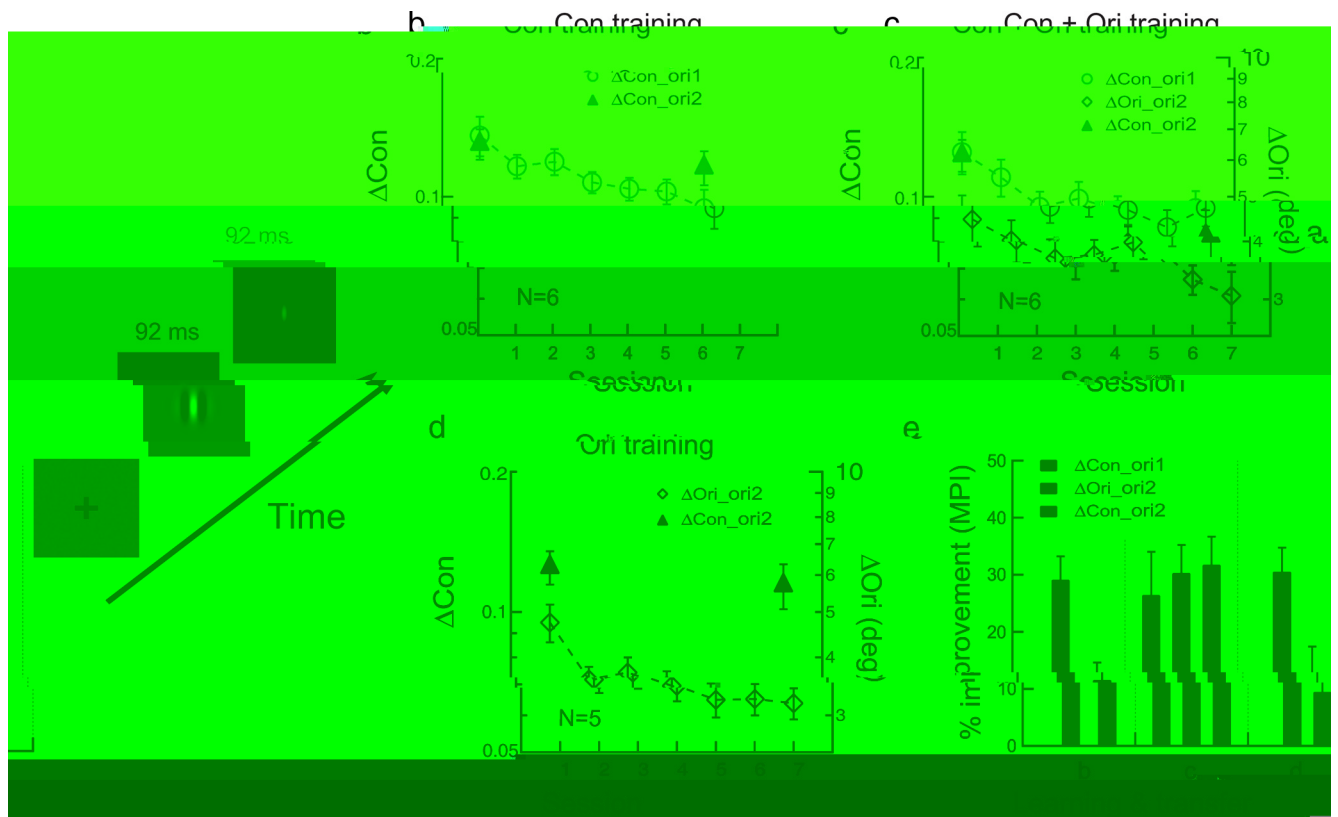
**Figure 1.** Perceptual learning of orientation discrimination and its transfer to a second orientation studied with TPE procedures. **a**, The stimulus configuration for orientation discrimination in which one interval contained a more clockwise Gabor stimulus. **b**, Successive TPE procedure. Phase 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 remeasured ( $126^\circ/36^\circ$ ,  $\Delta\text{ori\_ori2}$ , 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).

... ( $\Delta\text{ori\_ori2}$ ;  $t_{(14)} = 10.1$ ,  $p < 0.001$ ). 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...  
 ... TPE...  
 ...  $\Delta\text{ori\_ori1}$ ... TPE...  
 ...  $\Delta\text{ori\_ori2}$ ...  
 ...  $\Delta\text{ori\_ori1}$ , T... F... 2...  
 W...  
 TPE... F...  
 TPE...  
 ... 0, 15, 30, 45, ... 60...  
 ... (36... 126)...  
 ... T...  
 ... 2... A...  
 ...  
 W...  
 TPE... W...  
 (F... 1f). B... 30...  
 ... TPE...



**Figure 2.** Orientation specificity in contrast learning studied with conventional and TPE procedures. *a*, The stimulus configuration for contrast discrimination in which one interval contains a higher contrast Gabor stimulus. *b*, Conventional training. Contrast discrimination for a vertical or horizontal Gabor was practiced ( $\Delta\text{con\_ori1}$ ; green circles) and the transfer of learning was tested at an untrained orthogonal orientation ( $\Delta\text{con\_ori2}$ ; red triangles). *c*, TPE training. Contrast discrimination was practiced at ori1 ( $\Delta\text{con\_ori1}$ ; green circles); contrast thresholds indicated by the left ordinate and orientation discrimination (the exposure condition) was practiced at ori2 ( $\Delta\text{ori\_ori2}$ ; blue diamonds; orientation thresholds indicated by the right ordinate) in alternating staircases, and the transfer of learning for contrast discrimination was tested at ori2 ( $\Delta\text{con\_ori2}$ ; red triangles). *d*, Control. Orientation discrimination was practiced at the transfer orientation ( $\Delta\text{ori\_ori2}$ ; blue diamonds) and its impact on contrast discrimination was tested at the same orientation ( $\Delta\text{con\_ori2}$ ; red triangles). *e*, A summary of learning and transfer. Left, Conventional training in *b*; middle, TPE training in *c*; right, control in *d*.

**Orientation specificity and transfer in contrast learning**

To test whether the transfer of learning is orientation specific, we used a TPE procedure. Contrast discrimination was practiced at ori1 ( $\Delta\text{con\_ori1}$ ; MPI = 29.1 ± 4.1%,  $p < 0.001$ ) (Fig. 2*b,e*). Transfer of learning was tested at ori2 ( $\Delta\text{con\_ori2}$ ; MPI = 11.6 ± 3.0%,  $p = 0.006$ ), and orientation discrimination was practiced at ori2 ( $\Delta\text{ori\_ori2}$ ; MPI = 31.8 ± 4.9%,  $p = 0.001$ ) (Fig. 2*c*). Transfer of learning was tested at ori1 ( $\Delta\text{con\_ori1}$ ; MPI = 26.5 ± 7.5%,  $p = 0.008$ ) (Fig. 2*c,e*). Similarly, in the control condition, orientation discrimination was practiced at ori2 ( $\Delta\text{ori\_ori2}$ ; MPI = 31.8 ± 4.9%,  $p = 0.001$ ), and contrast discrimination was practiced at ori2 ( $\Delta\text{con\_ori2}$ ; MPI = 11.6 ± 3.0%,  $p = 0.006$ ). Transfer of learning was tested at ori1 ( $\Delta\text{con\_ori1}$ ; MPI = 26.5 ± 7.5%,  $p = 0.008$ ) (Fig. 2*d*). ANOVA ( $F(2, 10) = 10.0$ ,  $p = 0.001$ ) showed that the transfer of learning is orientation specific.

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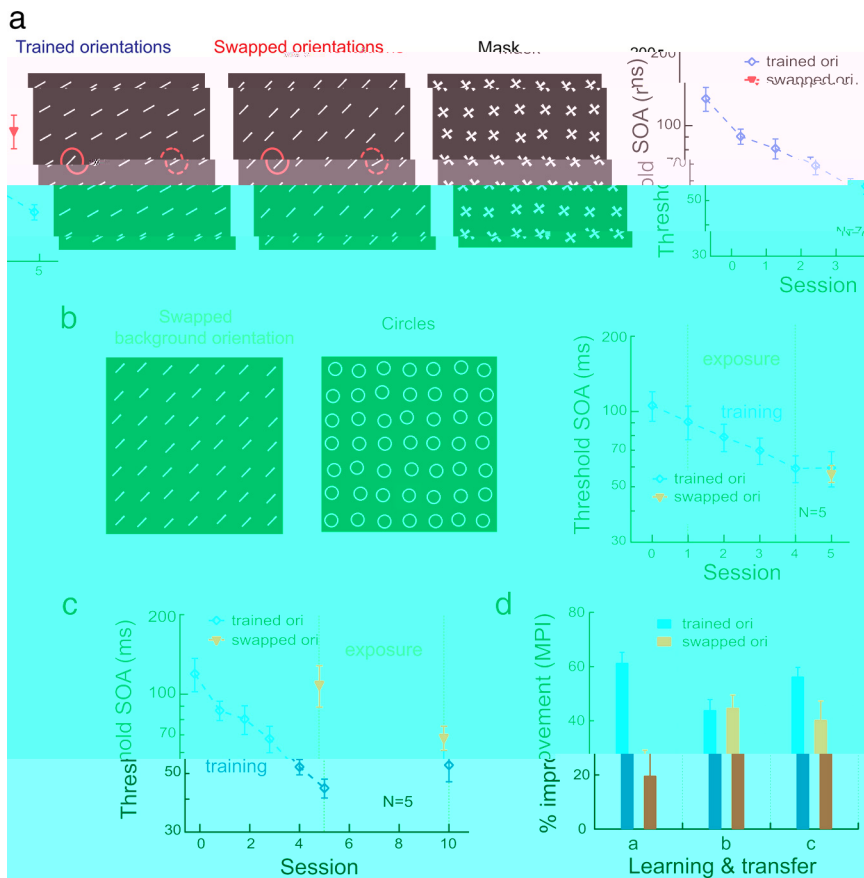
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**Orientation detection learning**

Orientation detection learning was studied with a TPE procedure. Contrast discrimination was practiced at ori1 ( $\Delta\text{con\_ori1}$ ; MPI = 29.1 ± 4.1%,  $p = 0.001$ ) (Fig. 2*b,e*). Transfer of learning was tested at ori2 ( $\Delta\text{con\_ori2}$ ; MPI = 11.6 ± 3.0%,  $p = 0.006$ ), and orientation discrimination was practiced at ori2 ( $\Delta\text{ori\_ori2}$ ; MPI = 31.8 ± 4.9%,  $p = 0.001$ ) (Fig. 2*c*). Transfer of learning was tested at ori1 ( $\Delta\text{con\_ori1}$ ; MPI = 26.5 ± 7.5%,  $p = 0.008$ ) (Fig. 2*c,e*). Similarly, in the control condition, orientation discrimination was practiced at ori2 ( $\Delta\text{ori\_ori2}$ ; MPI = 31.8 ± 4.9%,  $p = 0.001$ ), and contrast discrimination was practiced at ori2 ( $\Delta\text{con\_ori2}$ ; MPI = 11.6 ± 3.0%,  $p = 0.006$ ). Transfer of learning was tested at ori1 ( $\Delta\text{con\_ori1}$ ; MPI = 26.5 ± 7.5%,  $p = 0.008$ ) (Fig. 2*d*). ANOVA ( $F(2, 10) = 10.0$ ,  $p = 0.001$ ) showed that the transfer of learning is orientation specific.

specificity



**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)... (, 30, ...), I... (, 16, ...), T... A... H... (A... H... 1997, 2004), ... W... A... H... (MPI =  $61.4 \pm 3.9\%$ ,  $p < 0.001$ , ...) (MPI =  $19.7 \pm 9.5\%$ ,  $p = 0.041$ ) (E...

3a, ... A... A... H... T... MPI... W... TPE... SOA (106.7... I... 80% t... (E... 3b, t... (20% t... 60-t... T... (MPI =  $43.9 \pm 3.9\%$ ,  $p < 0.001$ )... (MPI =  $44.7 \pm 4.8\%$ ,  $p < 0.001$ ) (E... 3b, t... T... TI... TPE... (TI = 1.04)... (TI = 0.32) ( $p = 0.002$ , ... t... U... 8... E... 3a... (, ... (E... 3c). F... (MPI =  $9.6 \pm 6.9\%$ ;  $p = 0.12$ )... (E... 3c, ...). S... 33.9  $\pm$  5.3% ( $p = 0.002$ )... (10%)... (E... 3c, ...). T... MPI... 56.2  $\pm$  3.4% ( $p < 0.001$ )... 40.3  $\pm$  7.0% ( $p = 0.004$ )... ( $p = 0.12$ ).

**Discussion**

**Existing models of perceptual learning predicting specificity, not transfer**

T... (E... 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 DeYoe, 1996; Li and Gauthier, 2009). Although the TPE is located in the fusiform gyrus, it is distinct from the fusiform face area (FFA) (Gauthier and Tarr, 2002; Gauthier and Tarr, 2009). Although the TPE is located in the fusiform gyrus, it is distinct from the fusiform face area (FFA) (Gauthier and Tarr, 2002; Gauthier and Tarr, 2009). Although the TPE is located in the fusiform gyrus, it is distinct from the fusiform face area (FFA) (Gauthier and Tarr, 2002; Gauthier and Tarr, 2009).

**A rule-based learning model**

Our model is based on the idea that perceptual learning is a rule-based learning process. It involves the acquisition of specific rules that govern the perception of certain stimuli. This process is distinct from general perceptual learning, which involves the acquisition of general perceptual skills.

*Rule-based learning*

Expertise in visual perceptual learning (VPL) is characterized by a high level of accuracy and speed in identifying specific stimuli. This expertise is acquired through repeated exposure to the stimuli and the formation of specific rules that govern the perception of these stimuli. The model suggests that this process is distinct from general perceptual learning, which involves the acquisition of general perceptual skills.

*Rule application: specificity and transfer*

Our model predicts that perceptual learning is specific to the stimuli that are used during training. This specificity is due to the formation of specific rules that govern the perception of these stimuli. As a result, learning on one task does not necessarily lead to learning on a different task. However, there is some evidence for transfer of learning between related tasks (Tarr, 2001; Van der Geest et al., 2005; Gauthier et al., 2009). This transfer may be due to the formation of general perceptual skills that are shared across tasks.

Visual perceptual learning (VPL) is a process by which individuals become more accurate and faster at identifying specific stimuli. This process is distinct from general perceptual learning, which involves the acquisition of general perceptual skills. The model suggests that VPL is a rule-based learning process that involves the acquisition of specific rules that govern the perception of certain stimuli.

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