

Behavioral/Cognitive

Perceptual Learning at a Conceptual Level

R. Wang,^{1,2*} J. Wang,^{1*} J.-Y. Zhang,^{2*} X.-Y. Xu,^{2*} Y.-X. Xia,^{2*} S.-H. Li,¹ C. Yu,² and W. Li¹

¹State Key Laboratory of Cognitive Neuroscience and Learning and IDG/McGovern Institute for Brain Research, Beijing Normal University, Beijing 100875, China, and ²Department 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

Summary

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.

Introduction

Object learning is a process by which we learn to abstract and conceptualize the shared visual features defining an object category (Buckley and Gosselin, 2008). This learning is generalizable to transformations of familiar objects and even to new objects that differ in other physical properties (Gosselin and Buckley, 2004). 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 (Fahle, 2002). However, new training methods have shown complete VPL transfer across stimulus locations and orientations, suggesting the involvement of high-level cognitive processes (Chen et al., 2007; Li et al., 2009; Li and Wang, 2010; Li et al., 2011; Li and Wang, 2012; Li et al., 2013; Li and Wang, 2014; Li et al., 2015; Li and Wang, 2016). A recent study (Fahle and Poggio, 2006) demonstrated that VPL is transferable between different visual features (e.g., orientation and motion direction) when the training stimuli are presented in a way that encourages the formation of a high-level concept (Fahle and Poggio, 2006). This finding indicates that VPL can take place at a conceptual level and generalize to stimuli with different physical properties (Fahle and Poggio, 2006). Our findings thus reconcile perceptual and object learning into a unified framework (Fahle and Poggio, 2006).

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 (Fahle and Poggio, 2006).

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*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.

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... (H ... (W ... 1959, 1962). T ... VPL ... (Ka ... Sa ... 1991; S ... a ... 1995; T ... a ... Qa ... 2003), ... VI ... (M ... a ... Da ... a ... 1996; D ... a ... L ... 1999; La ... a ... G ... 2009).

H ... VPL ... (TPE) ... (Xa ... a ... 2008; J.Y. Z ... a ... a ... 2010; Z ... a ... a ... Ya ... 2014; X ... a ... a ... 2016) ... (Wa ... a ... a ... 2012). F ... a ... V ... (Wa ... a ... a ... 2012, 2014; J.Y. Z ... a ... a ... 2014). T ... I ... VPL.

T ... VPL ... I ... (...) ... T ... VPL ... I ... VPL ...

Ma ... a ... dM ... d

Observers and apparatus. S ... (33 ... 41 ...) ... A ... (... E ... 5G) ... T ... A ... D ... a ... H ... B ... N ... a ... U ... a ... P ... U ... T ... MATLAB ... P ... -3 ... (P ... 1997) ... a ... 21 ... S ... G520 ... (1024 ... × 768 ... 0.38 ... × 0.38 ... 120 H ... a ...) ... T ... a ... 50 ... / ... T ... a ... 8 ... a ... V ... (... = 17) ... A ... E ... A ... E ... II ... (SRR ...) ... (... E ... 5F).

Visual stimuli. T ... Ga ... (... E ... IA). T ... Ga ... 1.5 ... / ... 50% ... T ... SD ... Ga ... 0.67 ... T ... (S ... 1995) ... T ... 0.09 ... 0.37 ... T ... 18 ... (0.1 ...),

18 × 18 ... (0.16 × 0.16 ...). T ... 18 ... (1) ... a ... 8 ... 2 ... 6 ... 2 ... (3) ... 18 ... (4) ... 0, 0.04 ... A ... 18 ... F ...

T ... (...) ... (P ... Ha ... 2010). I ... 6.5 ... 4 ... T ... 5.5 ... 6.5 ...

Experimental procedure. I ... 2-a ... a ... 3- ... I- ... a ... 79.4% ...

I ... a ... 106 ... a ... 800 ...) ... a ... 500 ... ; ... 200 ...) ... F ... 35 ... 125 ... T ... F ... ±20% ... T ... 80% ... T ... 1.00, a ... T ...

A ... Ea ... 10 ... a ... (~50, 60 ...) ... T ... T ... T ... (a) ... 16 ... 10 ... I ... a ... (... E ... 5G), ... 5 ... I ... 4 ... A ... 200 ... 1.5 ... T ... A ... T ... 48 ... T ... (PSE) a ... 50%

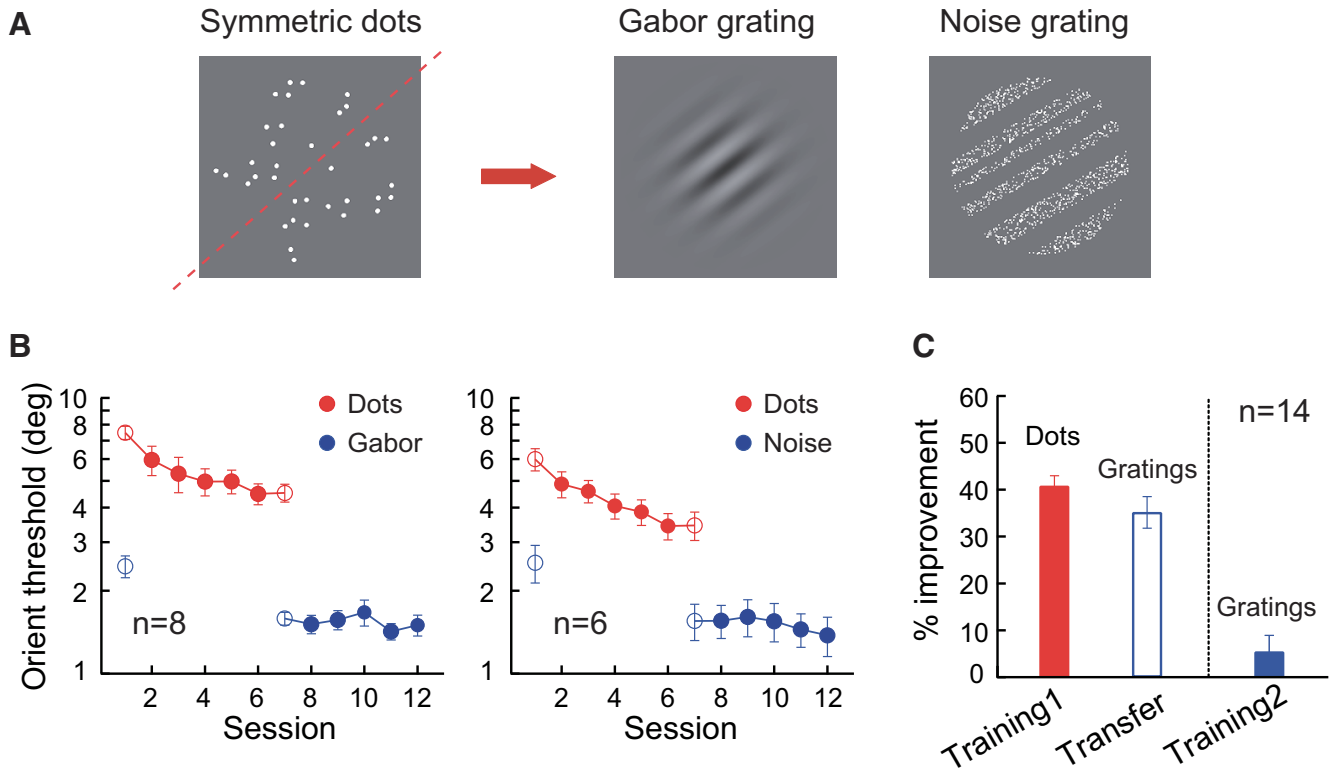


Figure 1. Transfer of orientation discrimination learning from symmetric dot patterns to gratings. **A**, Sample stimuli. The symmetry axis is indicated by the red dashed line (not shown in the actual stimuli). The arrow indicates the direction of learning transfer. **B**, Session-by-session mean discrimination 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 (“Training1” 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.

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Individuals were trained on a dot pattern orientation task (Fig. 1A). Performance improved over sessions (Fig. 1B). Transfer of learning was observed when subjects were tested on Gabor gratings (Fig. 1B, left) and noise gratings (Fig. 1B, right). Further training on gratings (Fig. 1C, right bar) improved performance on gratings (Fig. 1C, right bar) but did not affect performance on dot patterns (Fig. 1C, right bar).

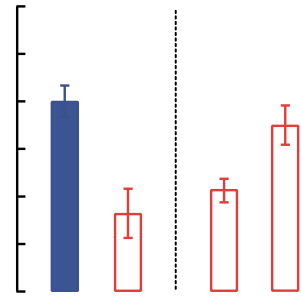
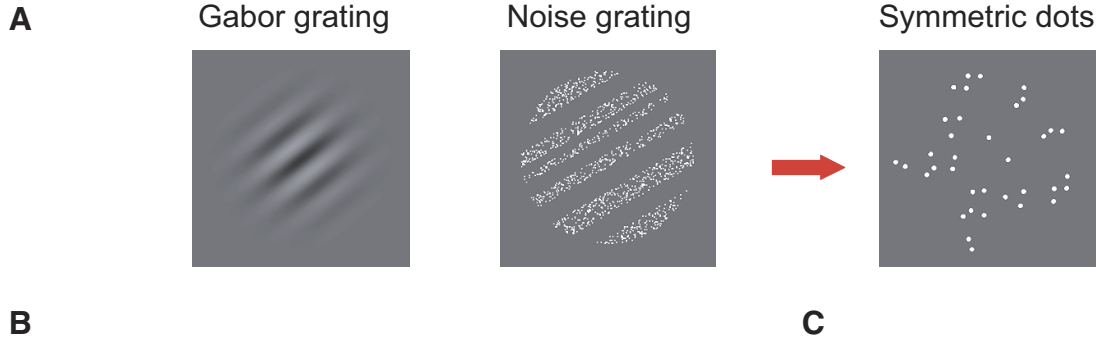
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(Fig. 1A). Further training on gratings (Fig. 1C, right bar) improved performance on gratings (Fig. 1C, right bar) but did not affect performance on dot patterns (Fig. 1C, right bar).

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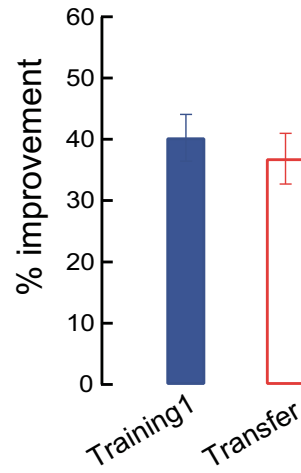
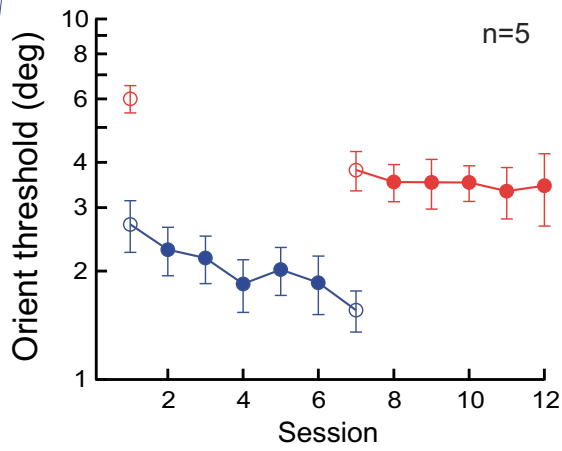
(16 subjects) (Fig. 1C, left bar) and noise gratings (Fig. 1C, right bar) (42.8 \pm 3.1%, p < 0.001, d = 3.62; Fig. 1B, C). A similar pattern of results was observed when Gabor gratings were used for training (Fig. 1B, left) and noise gratings were used for testing (Fig. 1B, right) (35.1 \pm 3.4%, p < 0.001, d = 2.78; Fig. 1B, C). Transfer of learning was observed when subjects were tested on Gabor gratings (Fig. 1B, left) and noise gratings (Fig. 1B, right) (5.4 \pm 3.5%, p = 0.15, d = 0.41; Fig. 1B, C). Individual learning curves are shown in Figure 1B. The percentage improvement was calculated as (pretraining threshold – posttraining threshold)/pretraining threshold. Error bars indicate \pm SEM.

125–135



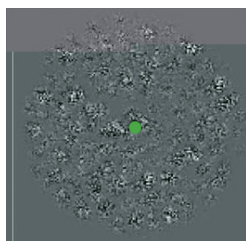
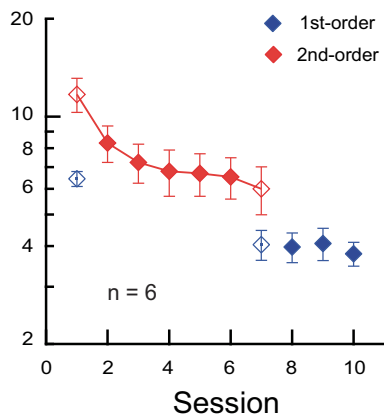
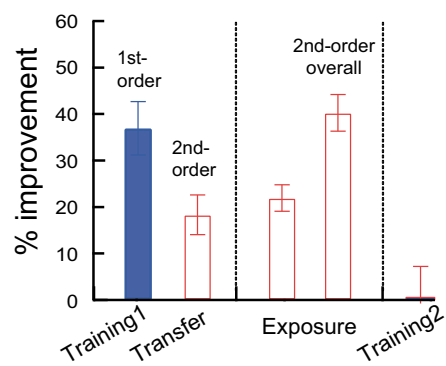
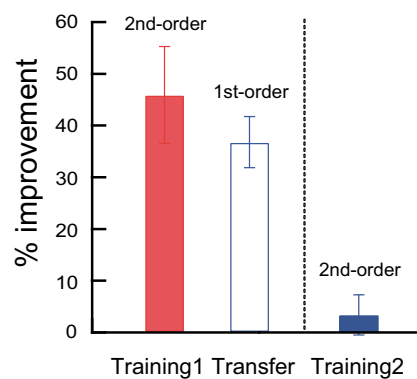
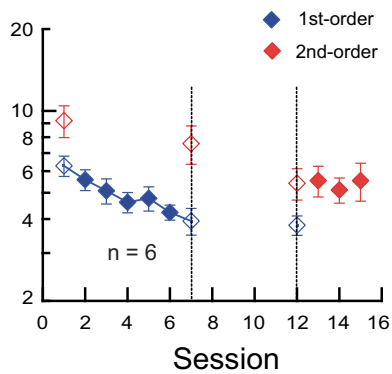
3.3% ($p < 0.001$, C ... $d = 3.24$; Fig. 2B,C). T...
 $16.4 \pm 5.2\%$ ($p = 0.007$, C ... $d = 0.85$; Fig. 2B,C), ...
 (Eq. 1).
 P... TPE...
 (98%), a...
 I...
 2/3. A...
 (5..., 16..., 50...),
 $21.8 \pm 2.4\%$ ($p < 0.001$, C ... $d = 2.38$; Fig. 2B,C). T...
 $35.0 \pm 4.1\%$ ($p < 0.001$, C ... $d = 2.27$; Fig. 2B,C), ...
 Fig. 1, B a C
 ($p = 0.18$, ... t ...; C ... $d = 0.38$). T...
 a..., 10..., 14... a...
 T...

$7.6 \pm 2.8\%$ ($p = 0.024$, C ... $d = 0.86$; Fig. 2C), ...
 TPE...
 I... TPE...
 5... TPE...
 (10... a...), 5... (Eq. 3). T...
 TPE...
 (..., ..., a...),
 (40.2 \pm 3.8%, $p < 0.001$, C ... $d = 2.87$) a...
 (36.9 \pm 4.2%, $p < 0.001$,
 C ... $d = 2.37$). E... a...
 (7.4 \pm 6.1%, $p = 0.28$, C ... $d = 0.33$). T...
 TPE...
 T... a...
 a... a... a... a...
 O... a... a... a...
 a... a... TPE...
 T... a... a... a...
 a... a... a... a...
 a... a... a... a...



(... M... a... M... ; Fig. 4A). I... a... a...
 ... (34.0 ± 5.1%, $p = 0.001$, $C_{\text{eff}} = 0.778$,
 $d = 2.724$), ... (9.7 ± 7.0%, $p = 0.22$, $C_{\text{eff}} = 0.57$),
 ... (26.3 ± 4.5%, $p = 0.002$, $C_{\text{eff}} = 2.37$). T... TPE...
 ... (-0.3 ± 5.8%, $p = 0.96$, $C_{\text{eff}} = 0.02$). T...
 ...
 W... a TPE... a... a... a... a...
 ... a... a... a... a... a... a... a... a... a...
 ... A... T...

... a... a... a... a... Fig. 4A... a...
 ... a... a... a... a... A...
 Fig. 4B, ... (a... a... a...
 ... a... a... a... a... a... a... a... a... a...
 ... (8.6 ± 4.5%, $p = 0.115$, $C_{\text{eff}} = 0.778$),
 ... a... a... a... a... a... a... a... a... a...
 ... (24.4 ± 7.3%, $p = 0.029$, $C_{\text{eff}} = 1.49$). C...
 ... a... a... a... a... a... a... a... a... a...
 ... a... a... a... a... a... a... a... a... a...
 ... T... 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**B****C****D**

Training1, a 1st-order neuron population, and a 2nd-order neuron population. Training1 (1st-order) neurons (Fig. 5A) and Training2 (2nd-order) neurons (Fig. 5B) were identified in the same brain section. The percentage of 1st-order neurons (blue diamonds) and 2nd-order neurons (red diamonds) was measured over 10 sessions (n = 6). The percentage of 1st-order neurons remained stable around 4-6%, while the percentage of 2nd-order neurons decreased from approximately 11% at session 1 to 6% at session 10.

(Laufer et al., 2001; Anderson et al., 2007). A 5% improvement in the 2nd-order neuron population (16 neurons) was observed after 6 sessions of training (45.9 ± 9.3% (p = 0.004, Cramer's d = 2.0; Fig. 5C), a significant improvement in the 2nd-order neuron population.

(36.8 ± 4.9%, $p = 0.001$, C_{or} 's $d = 3.0$). A 3 (a, b, c) × 2 (a, b) ANOVA revealed a main effect of condition ($F_{(2, 18)} = 10.7$, $p < 0.001$, $d = 0.58$),

Stimulus duration (36.9 ± 5.7%, $p = 0.001$, C_{or} 's $d = 2.6$; $F_{(1, 9)} = 15.5$),

and Stimulus duration × Condition interaction ($F_{(2, 18)} = 3.8$, $p = 0.028$, C_{or} 's $d = 1.76$). Tukey's

post hoc comparisons (Pillai's Trace, 2010). N = 10. Stimulus duration (18.3 ± 4.3%, $p = 0.008$, C_{or} 's $d = 1.76$). Tukey's

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post hoc comparisons (Pillai's Trace, 2010). N = 10. Stimulus duration (18.3 ± 4.3%, $p = 0.008$, C_{or} 's $d = 1.76$). Tukey's

D. c

Interactions, stimulus duration (36.9 ± 5.7%, $p = 0.001$, C_{or} 's $d = 2.6$; $F_{(1, 9)} = 15.5$),

and Stimulus duration × Condition interaction ($F_{(2, 18)} = 3.8$, $p = 0.028$, C_{or} 's $d = 1.76$). Tukey's

post hoc comparisons (Pillai's Trace, 2010). N = 10. Stimulus duration (18.3 ± 4.3%, $p = 0.008$, C_{or} 's $d = 1.76$). Tukey's

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