

Perceptual Learning at a Conceptual Level

Rui Wang,^{1,2*} Jie Wang,^{1*} Jun-Yun Zhang,^{2*} Xin-Yu Xie,^{2*} Yu-Xiang Yang,² Shu-Han Luo,¹ Cong Yu,² and Wu 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

Significance Statement

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

One of the remarkable functions of the brain is its capability to learn from past experience to improve cognitive and perceptual skills. Some forms of visual learning, such as recognition and categorization of complex objects, lead to abstraction of the rules defining the critical features of the object category (Bruner et al.,

1956; Rouder and Ratcliff, 2006). As a result, the learning effect can be generalized to a broad range of previously unseen objects that belong to the same learned category but are different in physical properties. Such cognitive ability is also important for invariant recognition of the same object under diverse viewing conditions. Conversely, visual perceptual learning (VPL)—improvement in discriminating subtle differences in basic visual features such as the orientation of a line or the moving direction of a dot—has long been regarded as a unique learning form because it is highly specific to the training conditions (Fahle, 2002). For example, the discrimination threshold (i.e., the just-noticeable difference) for a stimulus's orientation or moving direction is much reduced with training, but this learning effect usually disappears when the same stimulus is placed at a new visual field location or when its orientation/moving direction is rotated by 90 degrees (Crist et al., 1997). Such learning specificity coincides with the coding strategy in the primary visual cortex (V1), where different neurons represent different visual field lo-

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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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cations, stimulus orientations, and moving directions (Hubel and Wiesel, 1959, 1962). Therefore, VPL is often interpreted as training-induced changes specific to the subset of V1 neurons encoding the trained stimulus (Karni and Sagi, 1991; Schoups et al., 1995; Teich and Qian, 2003), or as improved readout of V1 sensory signals specifically activated by the trained stimulus (Mollon and Danilova, 1996; Doshier and Lu, 1999; Law and Gold, 2009).

However, our previous studies have shown that the location and orientation/direction specificity of VPL can be eliminated with new double-training or training-plus-exposure (TPE) procedures (Xiao et al., 2008; J.Y. Zhang et al., 2010; Zhang and Yang, 2014; Xiong et al., 2016) and that the learning effect can even transfer to the opposite visual field represented by the untrained brain hemisphere (Wang et al., 2012). For example, Vernier learning can transfer to a new location or orientation completely if the observers receive additional exposure of the new location or orientation via performing an irrelevant task (Wang et al., 2012, 2014; J.Y. Zhang et al., 2014). These results cannot be easily explained by specific changes in early visual cortical areas that are topographically organized to represent the visual field locations and to encode simple stimulus attributes such as line orientations and dot moving directions. Instead, a more central mechanism has to be introduced to account for the transfer of VPL.

The transferability of VPL is usually examined by comparing the same physical stimulus under the trained versus untrained conditions. It remains unknown whether the learning effect could generalize between different physical stimuli that define the same visual feature (e.g., a specific orientation or motion direction). This issue is particularly important because such learning transfer would suggest that VPL can take place at a conceptual level, similar to category or object learning. In this study, we investigated this possibility with the classical VPL tasks of orientation and motion direction discrimination.

Materials and Methods

Observers. Seventy-four naive observers (33 male and 41 female) with normal or corrected-to-normal vision were recruited from undergraduate and graduate students. All except four in a control experiment (see Fig. 5G) were inexperienced. They were required to sign an informed consent form before the study. All experimental procedures conformed to the Declaration of Helsinki and were approved by the ethics committees of Beijing Normal University and Peking University.

The stimuli were generated with a MATLAB-based Psychtoolbox-3 (Pelli, 1997) and presented on a 21 inch Sony G520 color monitor (1024 pixel \times 768 pixel, 0.38 mm \times 0.38 mm per pixel, 120 Hz frame rate). The mean luminance was 50 cd/m². The luminance of the monitor was linearized by an 8-bit look-up table. Viewing was binocular through a circular opening (diameter = 17°) of a piece of black cardboard that covered the rest of the monitor screen. A chin-and-head rest helped stabilize the head of the observer. Experiments were run in a dimly lit room. An EyeLink II eye tracker (SR Research) was used to monitor eye movements in a control experiment (see Fig. 5F).

Visual stimuli. The stimuli used for orientation discrimination training in the fovea included Gabor and noise grating patches and bilaterally symmetric dot patterns (see Fig. 1A). The Gabor gratings (Gaussian-enveloped sinusoidal gratings) were set at 1.5 cycles/° and 50% contrast, with the phase randomized for every presentation. The SD of the Gaussian envelop was 0.67°. The noise gratings (Schoups et al., 1995) consisted of pixelated stripes within a circular field (3° diameter). The widths and spacing of the stripes randomly varied between 0.09° and 0.37° and were re-randomized for each presentation.

The symmetric dot patterns consisted of 18 pairs of bilaterally symmetric white dots (0.1° diameter), which were confined to an area divided

into 18 \times 18 invisible square compartments (0.16° \times 0.16° each). The placement of the 18 dots on one side of the symmetry axis (within 18 rows by 9 columns of available compartments) was subject to the following constraints: (1) no dot was placed in the column of compartments nearest to the symmetry axis; (2) for the other 8 columns, 2 of them were randomly chosen to hold 3 dots in each column and each of the remaining 6 columns contained 2 dots; (3) only one dot was allowed in each of the 18 rows by randomly assigning row numbers to the 18 dots on one side of the symmetric pattern; and (4) the location of each dot was randomly jittered by 0–0.04° from the compartment center. After positioning the 18 dots on one side of the symmetry axis, the whole symmetric pattern was generated by placing another 18 mirror-imaged dots on the other side. For each stimulus presentation, the dot pattern was regenerated, preventing the observers from using local cues in the orientation discrimination task.

The stimuli used for motion direction discrimination in the fovea included luminance-modulated (i.e., first-order) stimuli and contrast-modulated (i.e., second-order) stimuli that were replicated from a previous study (Petrov and Hayes, 2010). In brief, a first-order stimulus was an additive combination of a radially isotropic moving modulator and a dynamic noise carrier, and a second-order stimulus was a multiplicative combination of the same moving modulator and noise carrier. The modulator had a diameter of 6.5°, contrast of 1, and moving speed of 4°/s. The edge of the modulator was blurred with a semitransparent linear ramp from 5.5° to 6.5° in diameter.

Procedure. In the orientation, motion direction, luminance, and contrast discrimination tasks, the thresholds were measured in a temporal 2-alternative forced-choice task using a 3-down 1-up staircase procedure that converged at a 79.4% correct response rate.

In each trial, the reference and test stimuli were randomly presented in two intervals (orientation or luminance task: 106 ms each; direction or contrast task: 800 ms) separated by an interstimulus interval (orientation or luminance: 500 ms; direction or contrast: 200 ms). For the orientation and motion direction discrimination tasks, the reference stimulus was set at 35° or 125° and the test stimulus was deviated from the reference by an amount automatically controlled by the staircase procedure. The observer's task was to judge in which interval the stimulus was tilted more clockwise. For the mean luminance discrimination task with the dot pattern stimuli, the luminance of individual dots was randomized within $\pm 20\%$ of a specific mean luminance level. This level was chosen in such a way that the mean luminance of the entire reference pattern was fixed at 80% of the screen maximal luminance. The mean luminance of the entire test pattern, which was lower, was controlled by a staircase. The observer's task was to report in which interval the dot pattern had a higher mean luminance. For the contrast discrimination task with the second-order motion stimuli, the contrast of the modulator in the reference stimulus was set at 1.00, and the contrast of the test stimulus was decreased by an amount controlled by a staircase. The observer's task was to report in which interval the stimulus had a higher contrast.

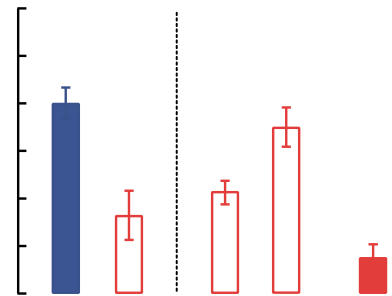
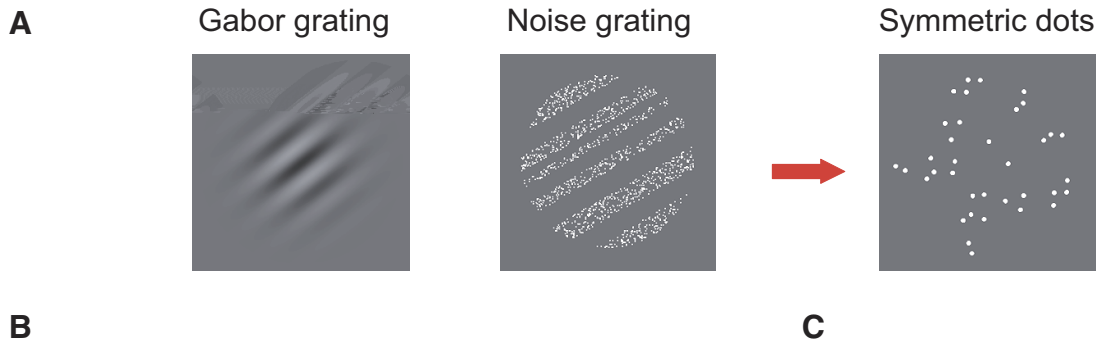
Auditory feedback was given on incorrect responses. Each staircase consisted of 10 reversals (~ 50 – 60 trials). The geometric mean of the last six reversals was taken as the discrimination threshold. The pretraining and posttraining thresholds were calculated based on six staircases. The mean thresholds in a training session (day) were calculated based on 16 or 10 staircases, as indicated in the text.

In a motion adaptation experiment (see Fig. 5G), the second-order motion stimulus at one of the training directions was first presented for 1 min as an adaptor at 5° retinal eccentricity left to the fixation point. It was then presented for 4 s at the beginning of each subsequent trial. After a 200 ms delay, a pair of identical first-order or second-order motion stimuli were presented for 1.5 s, one at the same adapted location and the other at a mirrored location in the opposite visual hemifield. The observers compared the speeds of the two stimuli by reporting which one moved faster. A method of constant stimuli was used to measure the perceived speed at the adapted location. The speed of the stimulus at the adapted location was the same as the adaptor speed. The speed of the other stimulus varied in seven levels from trial to trial. Each level consisted of 48 trials. The point of subjective equality (PSE) at 50% response rate was estimated by fitting the psychometric function with a

Weibull function. Control data with no adaptors were also collected as the baselines.

Results

In the orientation discrimination task, human observers were trained to discriminate a small difference in orientation between two otherwise identical stimuli that were displayed briefly and successively. The stimuli were either luminance gratings or bilaterally symmetric dot patterns (Fig. 1A). Processing of these two types of oriented stimuli is known to engage different visual cortical areas. The grating orientations are initially encoded in V1 (Hubel and Wiesel, 1959, 1962



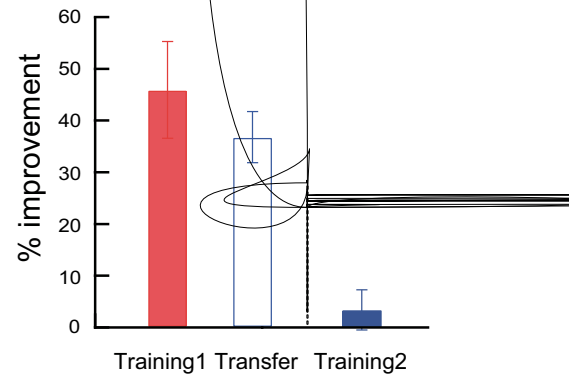
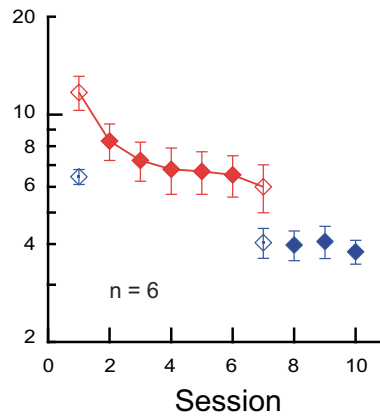
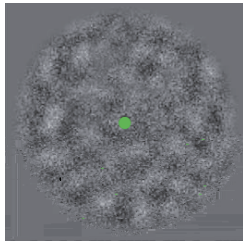
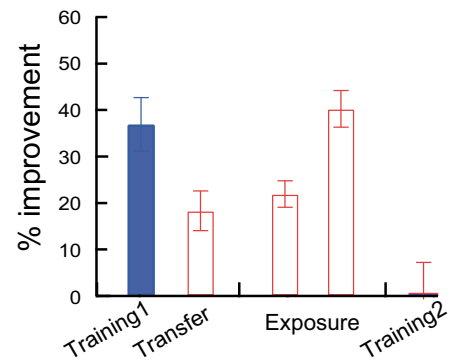
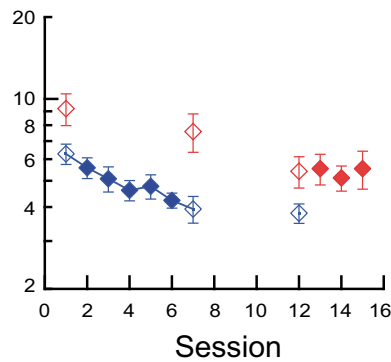
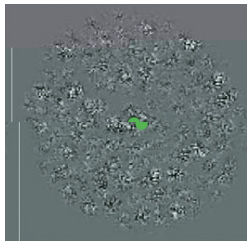
3.3% ($p < 0.001$, Cohen's $d = 3.24$; Fig. 2B,C). Training with the gratings also led to improved discriminability for the dot patterns by $16.4 \pm 5.2\%$ ($p = 0.007$, Cohen's $d = 0.85$; Fig. 2B,C), but at a rate that was less than half of the improvement when the dot patterns were trained directly (Fig. 1).

Previously, we applied double-training and TPE techniques to enable substantial, and often complete, learning transfer to untrained stimulus locations and orientations/directions (Xiao et al., 2008; J.Y. Zhang et al., 2010; Zhang and Yang, 2014; Xiong et al., 2016). Therefore, we suspected that similar techniques could also be effective for the current learning tasks. To test this possibility, we had the same observers subsequently exposed to the same-oriented symmetric dot patterns by performing an easy task (mean accuracy 98%) that was irrelevant to orientation discrimination. In this task, the observers judged which of the two consecutively displayed patterns contained more dots, with one pattern having the same number of dots as in the previous experiments and the other having only 2/3 of the dots. After this exposure phase (5 sessions, 16 blocks of 50 trials per session), dot pattern orientation discrimination was further improved by $21.8 \pm 2.4\%$ ($p < 0.001$, Cohen's $d = 2.38$; Fig. 2B,C). The overall improvement amounted to $35.0 \pm 4.1\%$ ($p < 0.001$, Cohen's $d = 2.27$; Fig. 2B,C), not significantly different from the improvement with direct training shown in Figure 1, B and C ($p = 0.18$, two-tailed independent t test; Cohen's $d = 0.38$). To determine whether the learning transfer was complete after the exposure phase, we called 10 of the 14 observers back to further practice dot pattern orientation discrimination for five sessions. This direct training only slightly improved the performance by

$7.6 \pm 2.8\%$ ($p = 0.024$, Cohen's $d = 0.86$; Fig. 2C), indicating that prior grating orientation learning had mostly transferred to dot patterns after applying the TPE procedure.

In addition to the above sequential TPE procedure, we also tested 5 more observers in a simultaneous TPE procedure in which training in grating orientation discrimination and the exposure of symmetric dot patterns were conducted within the same sessions in alternating block of trials (10 blocks each) for 5 sessions (Fig. 3). This procedure required only one pretest of dot pattern orientation threshold (before grating orientation training), unlike the previous sequential TPE procedure, in which two pretests of dot pattern orientation threshold (one before grating training, the other before dot pattern exposure) might have confounded the transfer effect. Grating orientation learning ($40.2 \pm 3.8\%$, $p < 0.001$, Cohen's $d = 2.87$) again mostly transferred to the dot patterns ($36.9 \pm 4.2\%$, $p < 0.001$, Cohen's $d = 2.37$). Five additional sessions of training in dot pattern orientation discrimination only resulted in a small and insignificant improvement ($7.4 \pm 6.1\%$, $p = 0.28$, Cohen's $d = 0.33$). Therefore, the results from both TPE procedures above showed that the enhanced orientation discriminability after training with gratings completely transferred to symmetrical dot patterns, just as the complete transfer in the reverse direction.

One may argue that the observers could covertly practice orientation discrimination with the dot patterns when they performed the easy task during the exposure phase in the TPE experiments. To exclude this possibility, we conducted a control experiment on a new group of observers by replacing the easy dot pattern exposure task (density identification) with a much more demanding one—near-threshold mean luminance discrimina-

A**B**

The same patterns of learning transfer were replicated in motion direction discrimination tasks. The stimuli were luminance-modulated (first-order) motion signals (Fig. 5A) detectable by local linear filters and contrast-modulated (second-order) motion signals (Fig. 5B) detectable only by nonlinear mechanisms

(Lu and Sperling, 2001; Ashida et al., 2007). After 5 sessions of practice (16 blocks of trials per session) with the second-order stimuli, 6 observers improved their direction discrimination of the second-order motion by $45.9 \pm 9.3\%$ ($p = 0.004$, Cohen's $d = 2.0$; Fig. 5C), and the learning significantly transferred to the

first-order stimuli ($36.8 \pm 4.9\%$, $p = 0.001$, Cohen's $d = 3.0$). A further 3 sessions of training with the first-order stimuli did not produce additional improvement ($5.3 \pm 3.7\%$, $p = 0.22$, Cohen's $d = 0.58$), suggesting that second-order motion discrimination learning transferred to the first-order motion completely.

Similar to the transfer of orientation discrimination learning from simple gratings to complex dot patterns, motion discrimination learning with the first-order stimuli ($36.9 \pm 5.7\%$, $p = 0.001$, Cohen's $d = 2.6$; Fig. 5D) in 6 observers initially only partially transferred to the second-order stimuli moving at the same direction ($18.3 \pm 4.3\%$, $p = 0.008$, Cohen's $d = 1.76$). This asymmetric learning transfer between first- and second-order motion was also reported previously (Petrov and Hayes, 2010). Nevertheless, after having the observers exposed to the second-order motion stimuli in a near-threshold contrast discrimination task (see Materials and Methods) for 5 sessions (16 blocks of 50–60 trials per session), their mean threshold for discriminating the second-order motion direction was further reduced by $22.0 \pm 2.9\%$ ($p < 0.001$, Cohen's $d = 3.1$), with a total improvement of $40.3 \pm 4.0\%$. Three sessions of subsequent direct training with the second-order stimuli did not induce further improvement ($-0.2 \pm 6.0\%$, $p = 0.75$, Cohen's $d = -0.15$), indicating that motion discrimination learning had completely transferred from the first- to the second-order stimuli.

A control experiment on another 5 naive observers showed that the exposure procedure by itself (contrast discrimination of the second-order motion stimuli for 5 sessions; Fig. 5E) did not produce any significant improvement in motion discrimination ($-1.1 \pm 2.5\%$, $p = 0.45$, Cohen's $d = -0.20$). This task specificity of learning also excluded the possibility that the performance improvement with second-order motion direction after the exposure phase was simply a result of exposure-based general learning; rather, it was the interaction between the exposure and the earlier first-order motion direction training that improved the perceptual sensitivity.

Our control experiments (Figs. 4, 5E) excluded the possibility that exposure to high-order stimuli alone could result in perceptual learning, indicating that exposure interacts with training of low-order stimuli to induce learning transfer. However, it remains mysterious exactly what roles the exposure plays in the TPE procedure. Previously, we showed that TPE can enable complete learning transfer to an untrained orthogonal orientation of the same stimulus (J.Y. Zhang et al., 2010). We now have evidence that the conventional orientation specificity could be a result of insufficient bottom-up stimulation of, or top-down attention to, the untrained stimulus orientation. Therefore, the exposure of the orthogonal orientation in the TPE procedure could amend these bottom-up and top-down issues to enable learning transfer (Xiong et al., 2015). Further studies are necessary to elucidate to what extent this understanding can apply to the current study and whether additional factors also come into play.

Our previous findings of learning transfer to untrained locations, orientations, and directions suggest that VPL is rule-based learning in that the learned reweighting rules can be applied to untrained conditions to allow learning transfer (Xiao et al., 2008; Wang et al., 2012, 2014; Zhang and Yang, 2014; Xiong et al., 2016). Our current data prompt us to speculate that the rules

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