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Perceptual learning of Vernier discrimination transfers from high to zero noise after double training

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ABSTRACT

Perceptual learning is often interpreted as learning of fine stimulus templates. However, we have proposed that perceptual learning is more than template learning, in that more abstract statistical rules may have been learned, so that learning can transfer to stimuli at different precisions. Here we provide new evidence to support this view: Perceptual learning of Vernier discrimination at high noise, which has thresholds approximately 10 times as much as those at zero noise, is initially non-transferrable to zero noise. However, additional exposure to a noise-free Vernier-forming Gabor, which is ineffective alone, not only maximizes zero-noise fine Vernier discrimination, but also further enhances high-noise Vernier performance. Such high-threshold coarse Vernier training cannot impact the fine stimulus template directly. One plausible explanation is that the observers have learned the statistical rules that can apply to standardized input distributions to improve discrimination, regardless of the original precision of these distributions.

1. Introduction

Practice improves a person's sensitivity to fine differences of basic visual features. This perceptual learning process has been attributed to neural tuning changes in early visual cortical neurons (Karni & Sagi, 1991; Fahle, Edelman, & Poggio, 1995; Schoups, Vogels, & Orban, 1995; Teich & Qian, 2003), or subsequent reweighting of the inputs from these neurons (Mollon & Danilova, 1996; Dosher & Lu, 1998, 1999; Yu, Klein, & Levi, 2004; Law & Gold, 2009; Dosher, Jeter, Liu, & Lu, 2013). These explanations are to some degree motivated or constrained by the frequent observations of learning specificities. That is, perceptual learning of various visual tasks is often specific to the trained retinal locations and feature dimensions (e.g., a specific orientation or motion direction).

However, in a series of double training studies, we have demonstrated that learning specificities can be significantly reduced or even completely abolished. For example, Vernier learning, which is very specific to the trained retinal location, can transfer completely to a new location if the observers also perform an irrelevant task (e.g., motion direction discrimination that by itself has no impact on Vernier discrimination) at the new location, either simultaneously with or after Vernier training (Xiao et al., 2008; Wang, Zhang, Klein, Levi, & Yu, 2012; Wang, Cong, & Yu, 2013; Wang, Zhang, Klein, Levi, & Yu, 2014). Even top-down attention to the new location without bottom-up stimulation, or bottom-up stimulation of the new location without observers' awareness, is effective (Xiong, Zhang, & Yu, 2016). Similar double training designs also work well to significantly reduce or remove orientation and motion direction specificities (Zhang et al., 2010; Zhang, Cong, Klein, Levi, & Yu, 2014; Zhang & Yang, 2014; Xiong, Xie, & Yu, 2016). In addition, double training is able to enable complete learning transfer to physically distinct stimuli, such as orientations defined by gratings vs. symmetric dot patterns, and directions by first- vs. second-order moving patterns, that are initially encoded by different neural mechanisms (Wang et al., 2016). We thus propose that perceptual learning is more likely rule-based learning. That is, some statistical rules of reweighting sensory inputs, such as reassigning weights on the basis of z-scores in standardized input distributions, are learned, so that learning can transfer to other stimulus conditions in principle (Xiao et al., 2008; Zhang et al., 2010; Wang et al., 2016). Moreover, perceptual learning may operate at a conceptual or semantic level (Wang et al., 2016).

In this study we targeted a unique format of learning specificity. First reported by Dosher and Lu (2005), and then confirmed by later studies (Lu, Chu, & Dosher, 2006; Huang, Lu, Tjan, Zhou, & Liu, 2007; Chang, Kourtzi, & Welchman, 2013; Chang, Mevorach, Kourtzi, & Welchman, 2014), perceptual learning of discriminating a visual feature imbedded in zero external noise, such as orientation, motion direction, or binocular disparity, can transfer to discrimination of the

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same feature imbedded in high external noise. However, learning of feature discrimination at high noise transfers much less or little to the same feature at zero noise.

We hypothesized that observers with feature discrimination training at both zero and high noise may learn the same rules of reweighting stimulus inputs, regardless of the dramatically different thresholds required for stimulus discrimination. More specifically, the observers learn to reweight standardized stimulus inputs, so that feature learning obtained at one noise level is in principle transferrable to a different noise level. This hypothesis is tested with a variation of the double training procedure in the current study. As its name stands, double training consists of two training tasks. One is the primary training task, which is Vernier training at high external noise here. The other is the secondary training task, which is orientation discrimination training here with a noise-free Gabor, a pair of which would form the Vernier stimulus. The outcomes of double training did show complete transfer of Vernier learning from high noise to zero noise.

2. Methods

The apparatus, stimuli, and procedures are identical to those used in a recently published study of ours (Xie & Yu, 2018). The relevant details are replicated here for readers' convenience.

2.1. Observers and apparatus

The observers consisted of 34 undergraduate and graduate students (18–27 years old, 15 males and 19 females) at Peking University with normal or corrected-to-normal vision. They were inexperienced in psychophysical observations and were unaware of the purposes of the experiments. Informed written consents, which were approved by the Peking University IRB, were collected before data collection. This work was carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

The stimuli were generated with Psychtoolbox-3 (Pelli, 1997) and presented on a 21-in CRT monitor (1024 pixel × 768 pixel, 0.39 mm × 0.39 mm pixel size, 120 Hz frame rate, and 33.4 cd/m^2 mean luminance). The screen luminance was linearized by an 8-bit look-up table. Viewing was through a circular opening (diameter = 17°) of a black cardboard that covered the rest of the monitor screen at a distance of 1 m. The head of the observers was stabilized with a chin-and-head rest. Experiments were run in a dimly lit room.

2.2. Stimuli

The Vernier stimulus consisted of two identical Gabors (Gaussian-windowed sinusoidal gratings) imbedded in various levels of external noise in a circular window (radius = 2°) (Fig. 1a), and was presented on a mean luminance screen background. The Vernier was centered on one visual quadrant at 5° retinal eccentricity. The two Gabors had the same spatial frequency (3 cpd), standard deviation (0.67°), contrast (0.47), orientation (vertical), phase (0°), and a center-to-center distance of 1.33°. To form a specific Vernier offset, the position of each Gabor shifted half the Vernier offset away in opposite directions perpendicular to the Gabor orientation. Each noise element was 4 × 4 pixel, with the luminance sampled from the look-up-table following a Gaussian distribution. The root mean square (rms) contrast of the external noise was 0%, 5%, 9%, 16%, or 29%. In actual experiments the Vernier and the noise stimuli were presented in alternating frames, with 6 frames each for a total duration of 100 ms.

The stimuli for orientation discrimination training were Gabors and bilaterally symmetric dot patterns centered in a quadrant diagonal to the Vernier stimulus at 5° retinal eccentricity. The Gabor was identical to those forming the Vernier stimulus. The symmetric dot pattern consisted of 18 pairs of bilaterally symmetric white dots (0.1° diameter), which were confined to an area divided into 18 × 18 invisible square compartments (0.16° × 0.16° each) (Fig. 3b). 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 reference orientation of the Gabor or symmetry axis was 36°.

2.3. Procedures

The Vernier threshold was measured with a one-interval staircase procedure. In each trial, a small fixation cross preceded the Vernier by 500 ms and stayed throughout the trial. The Vernier was presented for 100 ms. Observers reported whether the lower Gabor was to the left or right of the upper Gabor by key press. Auditory feedback was given on incorrect responses.

The orientation discrimination threshold was measured with a two-interval forced-choice staircase procedure. In each trial, a small fixation cross preceded the first interval by 500 ms and stayed throughout the trial. The Gabors or symmetric dot patterns at the reference orientation and the test orientation (reference + Δori) were shown in two 100-ms stimulus intervals, respectively, in a random order. The two stimulus intervals were separated by a 500-ms inter-stimulus interval. The observers judged which stimulus interval contained the more clockwise-oriented stimulus. Auditory feedback was given on incorrect responses.

Thresholds were estimated following a 3-down-1-up staircase rule that converged at a 79.4% correct response rate. Each staircase consisted of four preliminary reversals and six experimental reversals (approximately 50–60 trials). The step size of the staircase was 0.05 log units. The geometric mean of the experimental reversals was taken as the threshold for each staircase run.

In a pre- or post-training session, the Vernier thresholds at five noise contrasts were measured at two diagonal locations in a counterbalanced order, with each condition tested for 5 staircases, for a total of 50 staircases. These 50 staircases were completed in two daily sessions with the test sequence preset with a permuted table. The training sessions lasted six days, each consisting of 10 staircases of Vernier task at the highest noise and/or 10 staircases of an orientation discrimination task at zero noise and lasting for 1–1.5 h.

2.4. Experimental design & statistical analysis

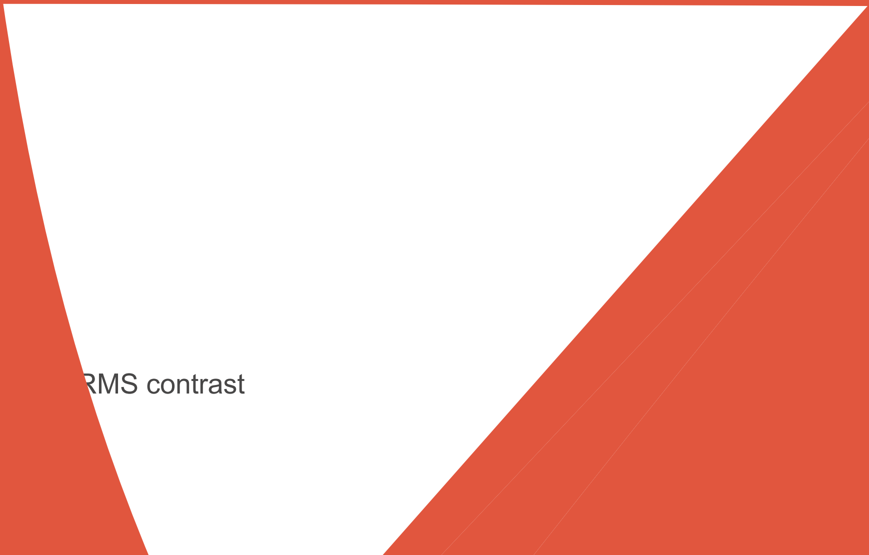
Sequential and simultaneous double training designs were used. Sequential double training consisted of 10 blocks (staircases) of Vernier training at the highest noise in the first six-day training phase, and 10 blocks of orientation discrimination training at zero noise in the second six-day training phase. Vernier performance at five noise levels and two Vernier and orientation training locations were measured, five blocks per condition, before and after each training phase. Simultaneous double training consisted of 10 blocks of Vernier task at the highest noise alternating with 10 blocks of orientation discrimination training at zero noise in the same daily session for six days. Vernier performance at five noise levels and two Vernier and orientation training locations were measured, five blocks per condition, before and after training.

Data were analyzed with SPSS 20 (SPSS INC, Chicago, IL, USA). The learning and transfer effects were measured by the percent threshold improvement from pre- to post-test sessions, which was $(\text{threshold}_{\text{pre}} - \text{threshold}_{\text{post}})/\text{threshold}_{\text{pre}}$. Repeated-measures ANOVAs tested the main effects of training, noise level, and stimulus location. Bonferonni corrections adjusted the estimate of the training effects at each noise level.

3. Results

Main experiments: Transfer of Vernier learning from high to zero noise with double training

First in a sequential double training experiment, seven observers initially completed baseline training, in which they practiced Vernier



1%, $F_{1,\ 7} = 68.09$,
$F_{1,\ 7} = 14.20$
$F_{1,\ 7} = 78$
rms contrast) ining lo
%, $F_{1,\ 7} = 15.23$, $p =$ ns
.6%, $F_{1,\ 7} = 23.85$, $p = 0.002$
5.7%, $F_{1,\ 7} = 61.37$, $p < 0.001$ at 0.
, Vernier thresholds at two lower noise contr ere
cantly improved at the Vernier training location .4 ± 7.3
9.32, $p = 0.019$ at 0 rms contrast, and 20.5 $F_{1,\ 7} =$
= 0.025 at 0.05 rms contrast), though not at n trai
cation (16.0 ± 11.0%, $F_{1,\ 7} = 2.12$, $p =$ 0
6.9 ± 8.2%, $F_{1,\ 7} = 4.21$, $p = 0.079$ at

We pooled data from both seque
training experiments to compare the
(Fig. 2d). A repeated-measures A
fects of training ($F_{1,\ 14} = 68.1$
$_{56} = 11.15$, $p < 0.001$), but
locations ($F_{1,\ 14} = 0.12$,
significant Vernier lea
$_{14} = 14.24$, $p = 0.00$
$p < 0.001$ at 0
$p < 0.001$ at
$p < 0.001$
$p < 0.00$
at zero
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and 47.6 ± 13.8%, $F_{1,\ 5} = 11.92$, $p = 0.018$ at 0.29 rms contrast). Therefore, to enable coarse-to-fine Vernier learning transfer, the stimulus in the secondary orientation training task needs to be the same Gabor to provide clear stimulus information.

3.3. Control 3: The effect of pre-test

In the earlier experiments, the pre-tests at the Vernier or orientation training location were completed with 25 blocks of trials at five noise contrasts, which alone could lead to threshold improvements. To measure the potential pretest effects, six new observers performed pre- and post-test Vernier tasks at five noise contrasts at two diagonal locations while skipping the training sessions. The pre- and post-tests were separated by about one week. The Vernier thresholds and improvements at the two locations were averaged. The results showed no significant main effects of training ($F_{1,\ 5} = 3.71$, $p = 0.112$) and noise contrast ($F_{4,\ 20} = 1.00$, $p = 0.431$), indicating minimal pre-test effects (Fig. 3c).

4. Discussion

Perceptual learning is often interpreted as training-induced neural plasticity in early sensory areas (Karni & Sagi, 1991; Schoups et al., 1995; Crist, Kapadia, Westheimer, & Gilbert, 1997), or post-receptor reweighting of sensory inputs that improves stimulus templates with no need of plasticity in the receptors per se (Mollon & Danilova, 1996; Dosher & Lu, 1998, 1999; Yu et al., 2004; Law & Gold, 2009; Dosher et al., 2013). Our study essentially extends the view of response reweighting by demonstrating that perceptual learning is more than learning of rigid stimulus templates. Rather the rules of reweighting the sensory inputs are learned that treat stimulus signals at zero and high noise equally even if the thresholds could be very different. This could be done through standardization of the distributions of visual inputs at different noise levels. This conclusion is in agreement with our general proposal that perceptual learning improves reweighting rules that are independent of stimulus location, feature dimension, physical properties, putative neuronal encoders, and threshold ranges (Xiao et al., 2008; Zhang et al., 2010; Wang et al., 2016), as well as of fineness or coarseness of the stimulus feature at various noise levels in the current case. These statistical reweighting rules apply to standardized stimulus distributions, rather than to raw stimulus data.

Several studies have investigated the brain mechanisms underlying fine feature learning at zero noise and coarse feature learning at high noise. Chowdhury and DeAngelis (2008) reported that training of fine disparity discrimination, which relies on ventral areas like V4 and IT, also improves a monkey's coarse discrimination. Moreover, coarse discrimination is no longer affected by temporal chemical inactivation of MT. Because the disparity tuning in MT neurons are unchanged, Chowdhury and DeAngelis (2008) attributed the changes to plasticity in downstream decision circuitries. Similarly, Chang et al. (2014) reported that after fine disparity learning, coarse disparity discrimination is no longer disturbed by TMS inactivation of the posterior parietal cortex, but both fine and coarse disparity discrimination is interrupted by inactivation of the lateral occipital cortex that only deals with fine disparity discrimination before training. Chang et al. (2014) thus made a specific assumption that training changes the weights of ventral and dorsal processing in coarse disparity discrimination, so that the ventral areas, which may store the learned stimulus template, now limit both fine and coarse feature discrimination.

Our new findings of two-way learning transfer between fine features at zero noise and coarse features at high noise provide new constraints and insights on the mechanisms of fine and coarse feature learning at different levels of noise. First, a precise stimulus template, regardless of where it is stored, would not predict coarse-to-fine learning transfer. The post-training Vernier thresholds at high noise were still many times as high as those at zero noise (Figs. 1 and 2), so learning with coarse Vernier could hardly improve the fine stimulus template. Second, the two-way transfer suggests that the plasticity may occur in brain areas that are untied to fine or coarse stimulus features. This possibility is consistent with Chowdhury and DeAngelis (2008) who suspected plasticity in downstream decision circuitries, as well as reports that relate perceptual learning mainly to changes in decision areas (Law & Gold, 2008; Kahnt, Grueschow, Speck, & Haynes, 2011). For example, Law and Gold (2008) reported that motion direction learning in monkeys is correlated to changes in decision area LIP neurons, but not to changes of motion area MT neurons. We predict that at least certain brain areas would make sensory decisions on the basis of standardized sensory inputs, which surely requires future neurophysiological and brain imaging evidence to elaborate.

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