



Contents lists available at [ScienceDirect](https://www.sciencedirect.com)

## Vision Research

journal homepage: [www.elsevier.com/locate/visres](http://www.elsevier.com/locate/visres)



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

Xin-Yu Xie, Cong Yu\*

*Psychology, McGovern Brain Research, and Center for Life Sciences, Peking University, China*

---

### ARTICLE INFO

*Keywords:*

Perceptual learning  
Vernier discrimination  
External noise  
Template

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.

---

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. M

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  $\times$  768 pixel, 0.39 mm  $\times$  0.39 mm pixel size, 120 Hz frame rate, and 33.4 cd/m<sup>2</sup> 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  $\times$  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  $\times$  18 invisible

square compartments (0.16°  $\times$  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.

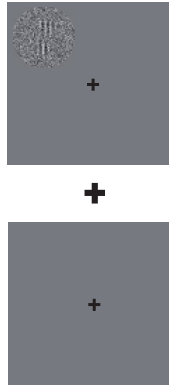
The orientation discrimination threshold was measured with a two-interval forced-choice staircase procedure. In each trial, a small fixation cross preceded the first interval by 500 ms and stayed throughout the

noise with double training

First in a sequential double training experiment, seven observers initially completed baseline training, in which they practiced Vernier discrimination at the highest noise contrast (rms contrast = 0.29) at one quadrant for six days. In pre- and post-training sessions, they completed the same Vernier task at a full range of noise contrasts (rms contrast = 0–0.29) at the training location and a diagonal transfer location (Fig. 1a). Training improved Vernier thresholds significantly at three higher noise contrasts at the training location ( $19.9 \pm 5.0\%$ ,  $F_{1,6} = 15.62$ ,  $p = 0.008$  at 0.09 rms contrast;  $23.7 \pm 6.7\%$ ,  $F_{1,6} = 12.44$ ,  $p = 0.012$  at 0.16 rms contrast; and  $32.2 \pm 10.1\%$ ,  $F_{1,6} = 10.14$ ,  $p = 0.019$  at 0.29 rms contrast), but not at two lower noise contrasts ( $-6.2 \pm 8.6\%$ ,  $F_{1,6} = 0.52$ ,  $p = 0.496$  at 0 rms contrast; and  $-0.7 \pm 9.7\%$ ,  $F_{1,6} = 0.01$ ,  $p = 0.942$  at 0.05 rms contrasts) (Fig. 1b, from pre to post1), consistent with Doshier and Lu (2005) that training at high noise had little impact on performance at low noise. At the untrained diagonal location, Vernier thresholds were also reduced at the highest noise contrast ( $28.0 \pm 9.8\%$ ,  $F_{1,6} = 8.20$ ,  $p = 0.029$  at 0.29 rms contrast) (Fig. 1b).

We suspected that the non-transfer of Vernier learning from high to zero noise was caused by the observers' lack of clear stimulus knowledge at zero noise, which was largely unavailable when the Vernier was imbedded in high noise. Therefore, as the second part of sequential double training, the same observers continued to practice an orientation discrimination task with a noise-free Gabor, two of which formed the Vernier pattern, at the diagonal location (Fig. 1a). This sequential

training reduced Vernier thresholds at two lower noise contrasts at both Vernier and orientation training locations ( $22.0 \pm 7.9\%$ ,  $F_{1,6} = 7.66$ ,  $p = 0.031$  at 0 rms contrast, and  $22.3 \pm 5.7\%$ ,  $F_{1,6} = 15.09$ ,  $p = 0.008$  at 0.05 rms contrast, at the Vernier training location; and  $20.0 \pm 4.9\%$ ,  $F_{1,6} = 16.64$ ,  $p = 0.007$  at 0 rms contrast, and  $27.1 \pm 5.6\%$ ,  $F_{1,6} = 23.41$ ,  $p = 0.003$  at 0.05 rms contrast, at the orientation training location) (Fig. 1b, from post1 to post2). Moreover, Vernier thresholds were further improved at three higher noise contrasts at the Vernier training location ( $16.3 \pm 6.2\%$ ,  $F_{1,6} = 6.84$ ,  $p = 0.040$  at 0.09 rms contrast,  $10.8 \pm 3.4\%$ ,  $F_{1,6} = 10.24$ ,  $p = 0.019$  at 0.16 rms contrast, and  $15.2 \pm 5.7\%$ ,  $F_{1,6} = 7.11$ ,  $p = 0.037$  at 0.29 rms contrast), as well as at the highest noise contrast at the orientation training location ( $18.0 \pm 4.5\%$ ,  $F_{1,6} = 15.63$ ,  $p = 0.008$  at 0.29 rms contrast), suggesting that direct Vernier training at high noise did not optimize the performance. The overall (post2 vs. pre) improvements at five noise levels from low to high were  $18.7 \pm 9.0\%$ ,  $22.8 \pm 8.4\%$ ,  $32.1 \pm 7.5\%$ ,  $31.8 \pm 7.0\%$ , and  $44.5 \pm 6.5\%$  at the Vernier training location, and  $25.2 \pm 6.1\%$ ,  $26.4 \pm 5.5\%$ ,



contrasts at the Vernier training location ( $25.6 \pm 3.1\%$ ,  $F_{1,7} = 68.09$ ,  $p < 0.001$  at 0.09 rms contrast,  $33.0 \pm 8.8\%$ ,  $F_{1,7} = 14.20$ ,  $p = 0.007$  at 0.16 rms contrast, and  $43.9 \pm 5.0\%$ ,  $F_{1,7} = 78.03$ ,  $p < 0.001$  at 0.29 rms contrast) and the orientation training location ( $29.1 \pm 7.4\%$ ,  $F_{1,7} = 15.23$ ,  $p = 0.006$  at 0.09 rms contrast,  $32.4 \pm 6.6\%$ ,  $F_{1,7} = 23.85$ ,  $p = 0.002$  at 0.16 rms contrast, and  $44.9 \pm 5.7\%$ ,  $F_{1,7} = 61.37$ ,  $p < 0.001$  at 0.29 rms contrast). Critically, Vernier thresholds at two lower noise contrasts were also significantly improved at the Vernier training location ( $22.4 \pm 7.3\%$ ,  $F_{1,7} = 9.32$ ,  $p = 0.019$  at 0 rms contrast, and  $20.5 \pm 7.2\%$ ,  $F_{1,7} = 8.14$ ,  $p = 0.025$  at 0.05 rms contrast), though not at the orientation training location ( $16.0 \pm 11.0\%$ ,  $F_{1,7} = 2.12$ ,  $p = 0.189$  at 0 rms contrast, and  $16.9 \pm 8.2\%$ ,  $F_{1,7} = 4.21$ ,  $p = 0.079$  at 0.05 rms contrast) (Fig. 2b, c).

We pooled data from both sequential and simultaneous double training experiments to compare the learning effects at five noise levels (Fig. 2d). A repeated-measures ANOVA indicated significant main effects of training ( $F_{1,14} = 68.17$ ,  $p < 0.001$ ) and noise contrast ( $F_{4,56} = 11.15$ ,  $p < 0.001$ ), but insignificant main effects between the two locations ( $F_{1,14} = 0.12$ ,  $p = 0.737$ ). The post-hoc analyses revealed significant Vernier learning at all noise levels ( $20.5 \pm 5.4\%$ ,  $F_{1,14} = 14.24$ ,  $p = 0.002$  at 0 rms contrast,  $21.4 \pm 4.4\%$ ,  $F_{1,14} = 23.26$ ,  $p < 0.001$  at 0.05 rms contrast,  $29.1 \pm 3.6\%$ ,  $F_{1,14} = 66.56$ ,  $p < 0.001$  at 0.09 rms contrast,  $30.0 \pm 4.4\%$ ,  $F_{1,14} = 46.70$ ,  $p < 0.001$  at 0.16 rms contrast, and  $44.0 \pm 3.5\%$ ,  $F_{1,14} = 157.22$ ,  $p < 0.001$  at 0.29 rms contrast). Moreover, the Vernier improvements at zero noise at two locations, as well as the direct Vernier training effect at zero noise ( $27.4 \pm 5.2\%$ ), were not significantly different among each other ( $F_{2,34} = 0.28$ ,  $p = 0.756$ , one-way ANOVA),

suggesting that double training likely maximized Vernier performance at zero noise. Here the direct Vernier training data were from a published experiment with the same pre- and post-tests as here, and with Vernier training at zero noise using the identical stimulus and procedure (Xie & Yu, 2018). These results together suggest that double training can enable learning transfer from high to zero noise and maximize Vernier performance at all noise levels, and the learning can transfer to the orientation-training location completely.

### 3.1. Control 1: The effect of secondary orientation training at high noise

In the above experiments, the stimulus with secondary orientation training was a Vernier-forming Gabor at zero noise. The purpose of using this noise-free Gabor was for the observers to obtain clear stimulus knowledge, so as to facilitate learning transfer from high noise to low noise. Two control experiments were performed to support this possibility. In the first control (Fig. 3a), seven new observers repeated the above simultaneous double training experiment, with the exception that the secondary orientation task was performed with the Gabor imbedded in the highest noise.

The new double training improved Vernier thresholds only at three higher noise contrasts at the Vernier training location ( $19.3 \pm 5.3\%$ ,  $F_{1,6} = 10.60$ ,  $p = 0.017$  at 0.09 rms contrast,  $13.8 \pm 6.2\%$ ,  $F_{1,6} = 4.93$ ,  $p = 0.068$  at 0.16 rms contrast, and  $28.9 \pm 4.1\%$ ,  $F_{1,6} = 48.74$ ,  $p < 0.001$  at 0.29 rms contrast) and the highest noise contrast at the orientation training location ( $20.7 \pm 6.9\%$ ,  $F_{1,6} = 9.06$ ,  $p = 0.024$  at 0.29 rms contrast) (Fig. 3a). Therefore, learning transfer from high noise to low noise did not happen when the same



and  $47.6 \pm 13.8\%$ ,  $F_{1, 5} = 11.92$ ,  $p = 0.018$  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. D c

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; Doshier & Lu, 1998, 1999; Yu et al., 2004; Law & Gold, 2009; Doshier 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.

## Ac

This research was supported by a Natural Science Foundation of China grant 31230030.

## R c

- Chang, D. H., Kourtzi, Z., & Welchman, A. E. (2013). Mechanisms for extracting a signal from noise as revealed through the specificity and generality of task training. *Journal of Neuroscience*, 33(27), 10962–10971.
- Chang, D. H., Mevorach, C., Kourtzi, Z., & Welchman, A. E. (2014). Training transfers the limits on perception from parietal to ventral cortex. *Current Biology*, 24(20), 2445–2450.
- Chowdhury, S. A., & DeAngelis, G. C. (2008). Fine discrimination training alters the causal contribution of macaque area MT to depth perception. *Neuron*, 60(2), 367–377.
- Crist, R. E., Kapadia, M. K., Westheimer, G., & Gilbert, C. D. (1997). Perceptual learning of spatial localization: Specificity for orientation, position, and context. *Journal of Neurophysiology*, 78(6), 2889–2894.
- Doshier, B. A., Jeter, P., Liu, J., & Lu, Z. L. (2013). An integrated reweighting theory of perceptual learning. *Proceedings of the National Academy of Sciences of the United States of America*, 110(33), 13678–13683.
- Doshier, B. A., & Lu, Z. L. (1998). Perceptual learning reflects external noise filtering and internal noise reduction through channel reweighting. *Proceedings of the National Academy of Sciences of the United States of America*, 95(23), 13988–13993.
- Doshier, B. A., & Lu, Z. L. (1999). Mechanisms of perceptual learning. *Vision Research*, 39(19), 3197–3221.
- Doshier, B. A., & Lu, Z. L. (2005). Perceptual learning in clear displays optimizes perceptual expertise: Learning the limiting process. *Proceedings of the National Academy of Sciences of the United States of America*, 102(14), 5286–5290.
- Fahle, M., Edelman, S., & Poggio, T. (1995). Fast perceptual learning in hyperacuity. *Vision Research*, 35(21), 3003–3013.
- Huang, X., Lu, H., Tjan, B. S., Zhou, Y., & Liu, Z. (2007). Motion perceptual learning: When only task-relevant information is learned. *Journal of Vision*, 7(10) 14 11–10.
- Kahnt, T., Grueschow, M., Speck, O., & Haynes, J. D. (2011). Perceptual learning and decision-making in human medial frontal cortex. *Neuron*, 70(3), 549–559.
- Karni, A., & Sagi, D. (1991). Where practice makes perfect in texture discrimination: Evidence for primary visual cortex plasticity. *Proceedings of the National Academy of Sciences of the United States of America*, 88(11), 4966–4970.
- Law, C. T., & Gold, J. I. (2008). Neural correlates of perceptual learning in a sensory-motor, but not a sensory, cortical area. *Nature Neuroscience*, 11(4), 505–513.
- Law, C. T., & Gold, J. I. (2009). Reinforcement learning can account for associative and perceptual learning on a visual-decision task. *Nature Neuroscience*, 12(5), 655–663.
- Lu, Z. L., Chu, W., & Doshier, B. A. (2006). Perceptual learning of motion direction discrimination in fovea: Separable mechanisms. *Vision Research*, 46(15), 2315–2327.
- Mollon, J. D., & Danilova, M. V. (1996). Three remarks on perceptual learning. *Spatial Vision*, 10(1), 51–58.
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, 10(4), 437–442.
- Schoups, A., Vogels, R., & Orban, G. A. (1995). Human perceptual learning in identifying the oblique orientation: Retinotopy, orientation specificity and monocularity. *Journal of Physiology*, 483(Pt 3), 797–810.
- Teich, A. F., & Qian, N. (2003). Learning and adaptation in a recurrent model of V1 orientation selectivity. *Journal of Neurophysiology*, 89(4), 2086–2100.
- Wang, R., Cong, L. J., & Yu, C. (2013). The classical TDT perceptual learning is mostly temporal learning. *Journal of Vision*, 13(5), 1–9 9.
- Wang, R., Wang, J., Zhang, J. Y., Xie, X. Y., Yang, Y. X., Luo, S. H., ... Li, W. (2016). Perceptual learning at a conceptual level. *Journal of Neuroscience*, 36(7), 2238–2246.
- Wang, R., Zhang, J. Y., Klein, S. A., Levi, D. M., & Yu, C. (2012). Task relevancy and demand modulate double-training enabled transfer of perceptual learning. *Vision Research*, 61, 33–38.
- Wang, R., Zhang, J. Y., Klein, S. A., Levi, D. M., & Yu, C. (2014). Vernier perceptual learning transfers to completely untrained retinal locations after double training: A “piggybacking” effect. *Journal of Vision*, 14(13), 1–10 12.
- Xiao, L. Q., Zhang, J. Y., Wang, R., Klein, S. A., Levi, D. M., & Yu, C. (2008). Complete

transfer of perceptual learning across retinal locations enabled by double training.