

Vernier perceptual learning transfers to completely untrained retinal locations after double training: A “piggybacking” effect

Rui Wang*

Department of Psychology, IDG/McGovern Institute for Brain Research, and Peking-Tsinghua Center for Life Sciences, Peking University, Beijing, China



Jun-Yun Zhang*

Department of Psychology, IDG/McGovern Institute for Brain Research, and Peking-Tsinghua Center for Life Sciences, Peking University, Beijing, China



Stanley A. Klein

School of Optometry and Helen Wills Neuroscience Institute, University of California, Berkeley, CA, USA



Dennis M. Levi

School of Optometry and Helen Wills Neuroscience Institute, University of California, Berkeley, CA, USA



Cong Yu

Department of Psychology, IDG/McGovern Institute for Brain Research, and Peking-Tsinghua Center for Life Sciences, Peking University, Beijing, China



Perceptual learning, a process in which training improves visual discrimination, is often specific to the trained retinal location, and this location specificity is frequently regarded as an indication of neural plasticity in the retinotopic visual cortex. However, our previous studies have shown that “double training” enables location-specific perceptual learning, such as Vernier learning, to completely transfer to a new location where an irrelevant task is practiced. Here we show that Vernier learning can be actuated by less location-specific orientation or motion-direction learning to transfer to completely untrained retinal locations. This “piggybacking” effect occurs even if both tasks are trained at the same retinal location. However, piggybacking does not occur when the Vernier task is paired with a more location-specific contrast-discrimination task. This previously unknown complexity challenges the current understanding of perceptual learning and its specificity/transfer. Orientation and motion-direction learning, but not contrast and Vernier learning, appears to activate a global process that allows learning transfer to untrained locations. Moreover, when paired with orientation or motion-direction learning, Vernier learning may be “piggybacked” by the activated global process to transfer to other untrained retinal

locations. How this task-specific global activation process is achieved is as yet unknown.

Introduction

Perceptual learning improves fine discrimination of various visual features such as contrast, orientation, spatial frequency, and motion direction. It has important implications for visual rehabilitation, for example, the treatment of amblyopia beyond the sensitive period. But the usefulness of perceptual learning is limited by location and feature specificity, in that a learned task often needs to be relearned when the stimulus is switched to a new retinal location, or to a new feature value, such as a new orientation or direction.

Location and feature specificities represent critical constraints on most perceptual learning theories. Many of these theories postulate that learning reflects neural plasticity in the retinotopic early visual cortex where neurons are most selective to basic visual features and their receptive fields are most localized (Karni & Sagi, 1991; Fahle, 1994; Schoups, Vogels, & Orban, 1995; Crist, Kapadia, Westheimer, & Gilbert, 1997; Bejjanki, Beck, Lu, & Pouget, 2011). Alternatively, training

Citation: 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):2, 1-10, <http://www.journalofvision.org/content/14/13/12>, doi:10.1167/14.13.12.

could reweight the responses of various activated sensory neurons to improve decision making (Mollon & Danilova, 1996; Doshier & Lu, 1999; Yu, Klein, & Levi, 2004; Petrov et al., 2005). There is also evidence that the degree of learning specificity may be determined by the task difficulty or precision (Ahissar & Hochstein, 1997; Jeter, Doshier, Petrov, & Lu, 2009). The reverse hierarchy theory thus suggests that perceptual learning of easy visual tasks is location and feature nonspecific and cognitive, and is accomplished at high levels of the information processing hierarchy. In contrast, learning of difficult tasks is location and feature specific, and is accomplished at the bottom of the hierarchy, perhaps as early as V1 (Ahissar & Hochstein, 1997).

However, in recent studies we have employed a “double training” technique to enable learning transfer to a new location (Xiao et al., 2008; Wang, Zhang, Klein, Levi, & Yu, 2012; Wang, Cong, & Yu, 2013), as well as a logically similar “training-plus-exposure” (TPE) technique to enable learning to transfer to a new feature value, i.e., a new orientation or motion direction (J. Y. Zhang et al., 2010; J. Y. Zhang, Cong, Klein, Levi, & Yu, 2014; J. Y. Zhang & Yang, 2014). The learned tasks include contrast, orientation, Vernier, motion direction, and texture discrimination, which are all difficult and high precision tasks at threshold levels. The significant and often complete learning transfer challenges the very basic concepts of location and feature specificities in perceptual learning, as well as various theories that are constrained by these specificities. We thus suggested that visual perceptual learning, regardless of task difficulty and precision, is mainly a rule-based process that occurs in high-level brain areas beyond the retinotopic and orientation-selective visual cortex (J. Y. Zhang et al., 2010).

Several theories have been proposed to explain the location transfer of learning through double training, in which location-specific learning can significantly and often completely transfer to a new location where an irrelevant task is also trained. Our original speculation was that double training might improve spatial attention to an untrained location, so that high-level learning can functionally connect to the attention-potentiated neurons at that location for learning transfer (Xiao et al., 2008). More recently, Solgi, Liu, and Weng (2013) proposed that when the observers are “off-task” (i.e., not practicing or attending to the stimuli), prior exposure to the transfer location through double training triggers self-organization of connections from learned high-level concept neurons to low-level sensory neurons at the transfer location. These off-task processes play a major role in improving performance at the transfer location. In addition, Doshier and Lu recently revised their integrated reweighting theory by adding high-level, location-

independent representations to the learning network to explain learning transfer to other locations (Doshier, Jeter, Liu, & Lu, 2013). Like location-specific representations, these high-level broadly tuned representations are also reweighted through training, so that location transfer of learning can be realized through up-regulation of location independent weights via double training of tasks that requires broad tuning (Liu, Lu, & Doshier, 2011).

The current study began as a more comprehensive survey of double training related learning transfer. However, the results, some of which were obtained with modified training paradigms as the study proceeded, describe a surprisingly complex picture of specificity and transfer in perceptual learning. This complex picture cannot be easily explained by current perceptual learning theories, including the recent ones described above. We hope that these surprising data will attract new research that will bring new insights into the understanding of perceptual learning. We also hope that the new training paradigms will help guide the development of more efficient protocols for clinical visual training and rehabilitation.

Methods

Observers and apparatus

Data presented in this paper were collected from 76 observers (undergraduate students in their early 20s). All had normal or corrected-to-normal vision, and were new to psychophysical testing and naïve to the purposes of the study. Informed written consent was obtained from each observer prior to data collection.

The stimuli were generated with a Matlab-based WinVis program (Neurometrics Institute, Oakland, CA) and presented on a 21-in. Sony G520 color monitor (for Vernier and contrast stimuli: 2048 pixel × 1536 pixel, 0.19 mm (H) × 0.19 mm (V) per pixel, 75 Hz frame rate; for motion and orientation stimuli: 1024 pixel × 768 pixel, 0.38 mm (H) × 0.38 mm (V) per pixel, 120 Hz frame rate). The mean luminance was 50 cd/m². The luminance of the monitors was linearized by an 8-bit look-up table. Viewing was monocular, and a chin-and-head rest helped stabilize the head of the observer. Experiments were run in a dimly lit room.

Stimuli

The Vernier stimulus consisted of a pair of identical Gabors (Gaussian-windowed sinusoidal gratings) on a mean luminance screen background, which was centered in one retinal quadrant (Figure 1a). The two

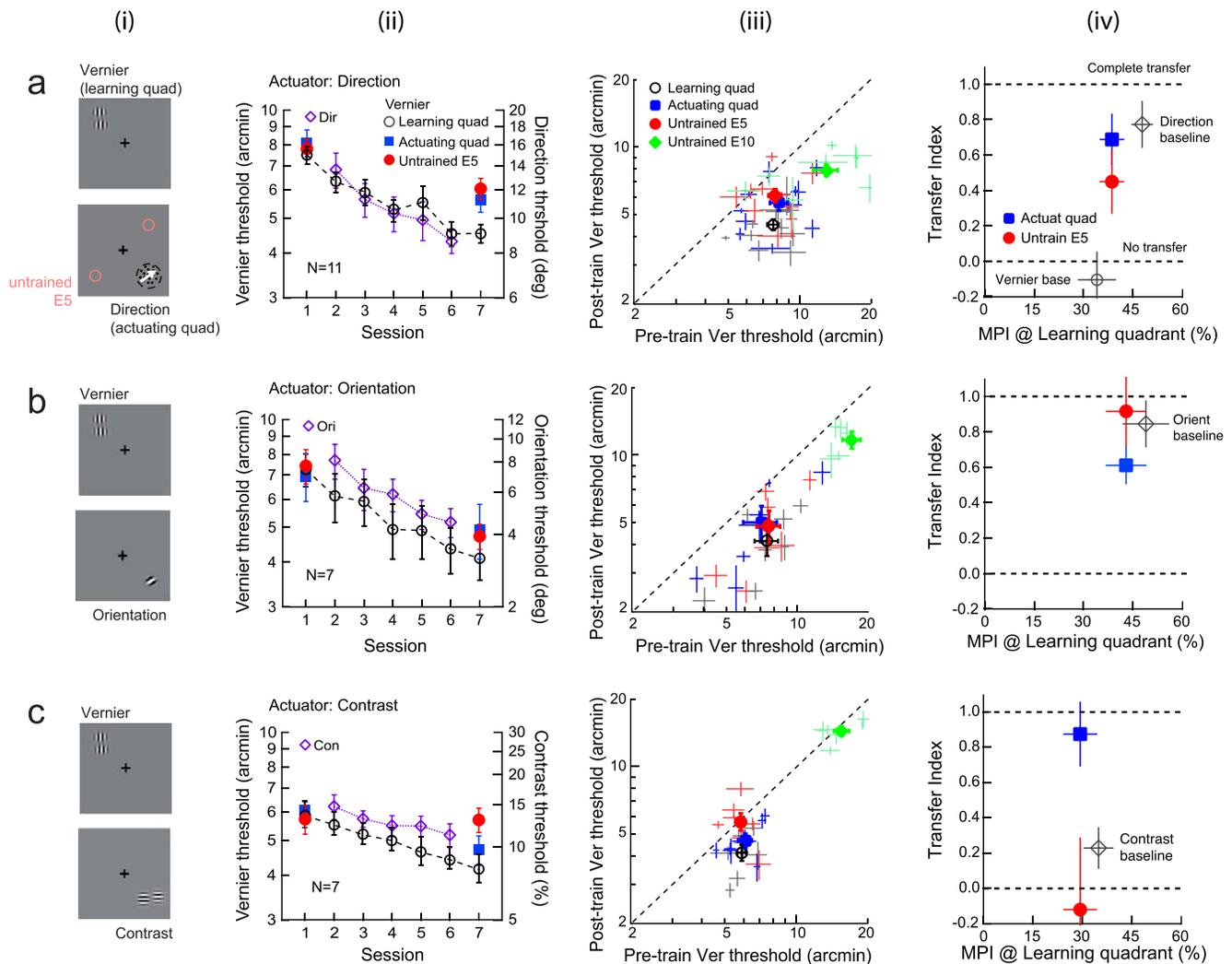


Figure 1. Transfer of Vernier learning to completely untrained quadrants after paired with different actuators: (a) motion direction learning; (b) orientation learning; and (c) contrast learning, at diagonal actuating quadrants. The transfer of Vernier learning was tested at the actuating quadrant and the untrained quadrants at the same 5° eccentricity (Untrained E5) or a different 10° eccentricity (Untrained E10). (i): Stimuli. The pink circles (not shown in actual stimuli) indicate stimulus locations at the untrained quadrants at 5° eccentricity. (ii): The mean session-by-session changes of thresholds. (iii): Pre- and posttraining comparisons of mean and individual Vernier thresholds at the learning and the untrained quadrants. (iv): Transfer Indices for Vernier learning with paired, as well as for unpaired baseline Vernier, direction, orientation, and contrast learning. The abscissa indicates the MPIs of various learning conditions at the learning quadrant.

Gabors had the same spatial frequency (3 cpd), standard deviation (0.29°), contrast (0.47), orientation (either vertical or horizontal), and a center-to-center distance of 4λ. 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. The same Vernier stimulus was also used for contrast-discrimination training unless otherwise specified, with the Vernier offset jittered at ±15 arcmin. The contrasts of the two Gabors were set at 0.47 and 0.47 + ΔC. The viewing distances for all stimuli presented at 5° and 10° eccentricities were 1.5 m and 0.75 m, respectively.

The motion stimulus consisted of 25 black random dots (4 × 4 pixels each) in an invisible (mean luminance) 2°-diameter circular window centered in one retinal quadrant (Figure 1a). Each dot had a lifetime of 250 ms. When a dot reached its lifetime or traveled out of the stimulus window, a new dot was generated from the other side of the window at a random position following the same lifetime rule. All dots moved in the same direction (36° or 126°) at a speed of 7°/s. Outside the circular window was the mean luminance monitor screen.

The stimulus for orientation discrimination was a Gabor patch (spatial frequency = 1.5 cpd, standard

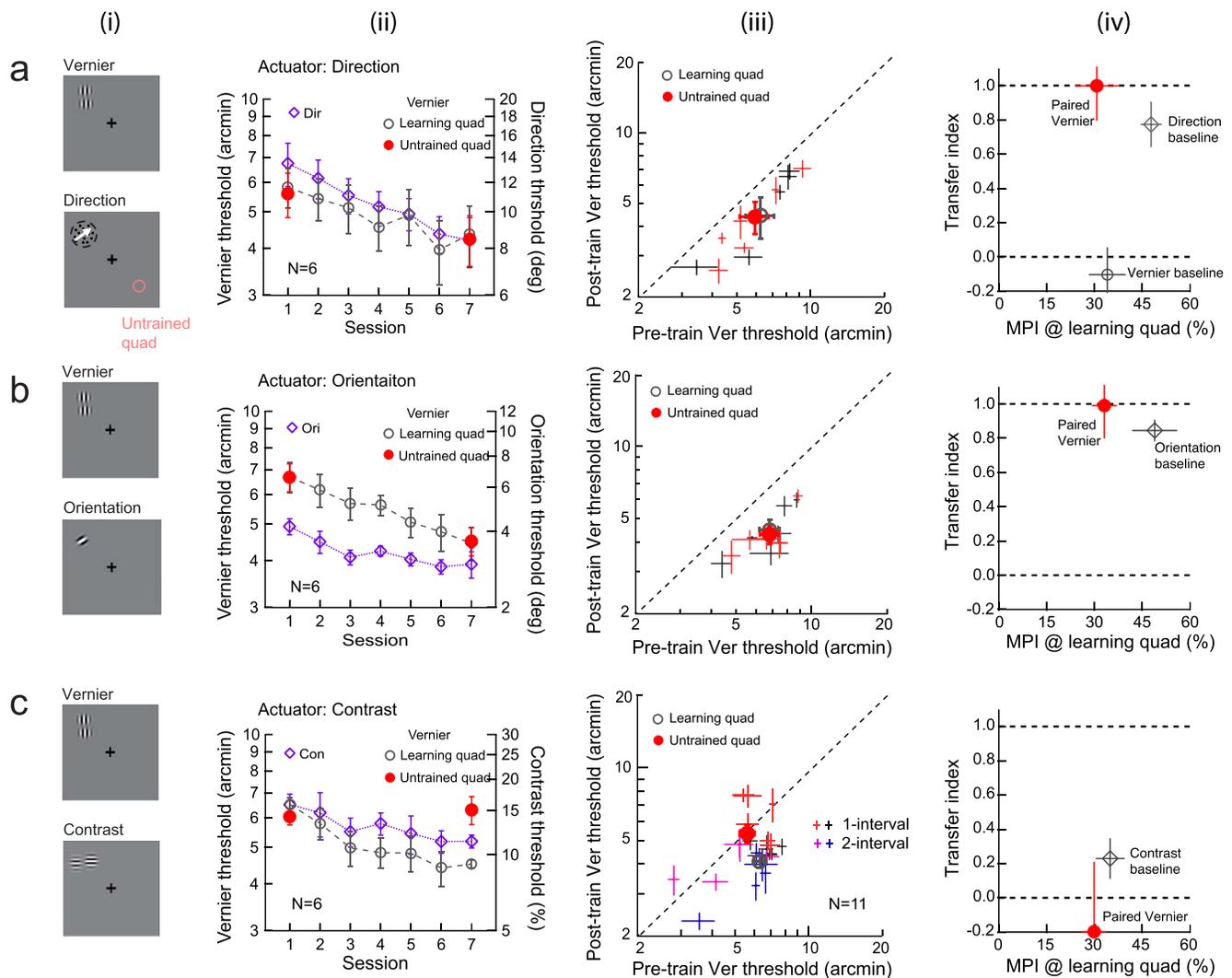


Figure 2. Transfer of Vernier learning after paired with different actuators at the same retinal location: (a) Paired with motion-direction learning; (b) with orientation learning; (c) with contrast learning. The transfer of Vernier learning was tested at a completely untrained diagonal quadrant. (i): Stimuli. The pink circles (not shown in actual stimuli) indicate the stimulus locations at the untrained quadrants. (ii): The mean session-by-session changes of thresholds. (iii): Pre- and posttraining comparisons of mean and individual Vernier thresholds at the learning and the untrained quadrants. (iv): Transfer Indices for the Vernier learning with paired, as well as for unpaired baseline Vernier, direction, orientation, and contrast learning. The abscissa indicates the MPIs of various learning conditions at the learning quadrant. Note: Figure 2c-ii only shows data from six observers who performed two Gabor contrast discrimination with single-interval 2AFC trials. Figure 2c-iii shows data from these six observers (black and red bars) and five additional observers who performed single Gabor contrast discrimination with two-interval 2AFC trials (blue and pink bars). Figure 2c-iv shows mean transfer index from all eleven observers.

deviation = 0.29°, orientation = 36° or 126°, contrast = 0.47, and phase randomized for every presentation) on a mean luminance background centered in one retinal quadrant (Figure 1b). Stimuli were viewed through a circular opening (diameter = 17°) of a black cardboard that covered the entire monitor screen. This control minimized external cues (e.g., monitor edges) the observers could use to determine the orientations of the stimuli. The same Gabor patch was also used in one occasion for contrast-discrimination training (Figure 2c-iii).

Procedure

Vernier thresholds, as well as contrast-discrimination thresholds of Vernier stimuli, were measured with a single-interval staircase procedure. In each trial, the stimulus was presented for 200 ms. For Vernier discrimination, an observer judged whether the right Gabor was higher or lower than the left Gabor for a horizontal Vernier, or the lower Gabor was to the left or right of the upper Gabor for a vertical Vernier. For contrast discrimination, an observer judged which of the

two Gabors had a higher contrast. A small foveal fixation cross preceded each trial by 500 ms and stayed through the trial. As a control, we also measured contrast-discrimination thresholds with a single Gabor patch in a temporal 2-interval forced-choice procedure (Figure 2c-iii). Auditory feedback was given on incorrect responses.

Direction discrimination thresholds were measured with a temporal 2-interval forced-choice (2-IFC) staircase procedure. In each trial, the reference and test (reference direction + Δ direction) were separately presented in two 500 ms stimulus intervals in a random order separated by a 500 ms interstimulus interval. The observer's task was to judge in which interval the random dots moved in a more clockwise direction. A small fixation point preceded each trial by 300 ms and stayed through the trial. Auditory feedback was given on incorrect responses.

Orientation discrimination thresholds were measured with a temporal 2-interval forced-choice (2-IFC) staircase procedure. In each trial, the reference and test (reference + Δ orientation) were separately presented in the two 100-ms stimulus intervals in a random order separated by a 500-ms interstimulus interval. The observer's task was to judge which stimulus interval contained more clockwise orientation. A small fixation point preceded each trial by 400 ms and stayed through the trial. Auditory feedback was given on incorrect responses.

Thresholds were estimated using a classical 3-down-1-up staircase rule that resulted in a 79.4% convergence level. 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.

Statistical analyses

The performance improvement due to training or transfer was represented by percent improvement (PI). $PI = 100\% \times (Th_{pre} - Th_{post}) / Th_{pre}$. Here Th_{pre} stood for pretraining threshold, and Th_{post} stood for posttraining threshold.

A transfer index (TI) defined by $TI = MPI_{transfer} / MPI_{trained}$ was used to compare the transfer of learning among different training conditions, in which MPI stood for mean percent improvement. $TI = 1$ indicated complete transfer and $TI = 0$ indicated no transfer.

Two-tailed paired t tests were used to test the possibility that the posttraining thresholds were significantly different from the pretraining thresholds in the same observers, and to compare TI values against $TI = 1$ or $TI = 0$. The p value was labeled as p_1 when TI values were tested against $TI = 1$, and as p_0 when TI values were tested against $TI = 0$. In addition, a one-

way ANOVA contrast test was used to compare TIs among different groups of observers.

Research design

This study consisted of three double-training experiments. In the first experiment, Vernier training was paired with training of motion-direction discrimination ($N = 11$), orientation discrimination ($N = 7$), or contrast discrimination ($N = 7$) in two diagonal quadrants, respectively (Figure 1). In the second experiment, Vernier training was paired with training of motion-direction discrimination ($N = 6$), orientation discrimination ($N = 6$), or contrast discrimination ($N = 11$) in the same diagonal quadrant (Figure 2). In both experiments the two tasks were trained in the same sessions in alternating blocks of trials (staircases). In the third experiment, Vernier training was performed either before ($N = 6$) or after ($N = 6$) orientation-discrimination training in a sequential double training paradigm (Figure 3). In addition to these double training experiments, one-training conditions were also performed as baseline measures. These conditions included motion-direction training ($N = 6$), orientation training ($N = 6$), and contrast training ($N = 5$) (data presented in Figures 1 and 2). The Vernier baseline measure was part of the sequential double training condition in Figure 3.

New naïve observers were recruited for each experiment. They all practiced for 20 trials to familiarize themselves with the training task before the training formally started. Each pre- or posttraining session consisted of two conditions for single training and three conditions for double training. Each condition was measured for five staircases (approximately 250–300 trials). All 10 or 15 staircases were run following a randomly permuted table for each observer. The duration varied from 1 to 1.5 hr, depending on the conditions. Each training session consisted of 16 staircases and lasted about 1.5 hr on a single day. More details can be found in the Results section below.

Results

Orientation and motion signals actuate perceptual learning to transfer to untrained locations

Three groups of observers were trained with a highly location-specific Vernier task in one visual quadrant at 5° retinal eccentricity (the “learning quadrant,” Figure 1a). Each group was also trained in the same sessions with one of the secondary training tasks (the “actuator” task) in the diagonal visual quadrant at the same

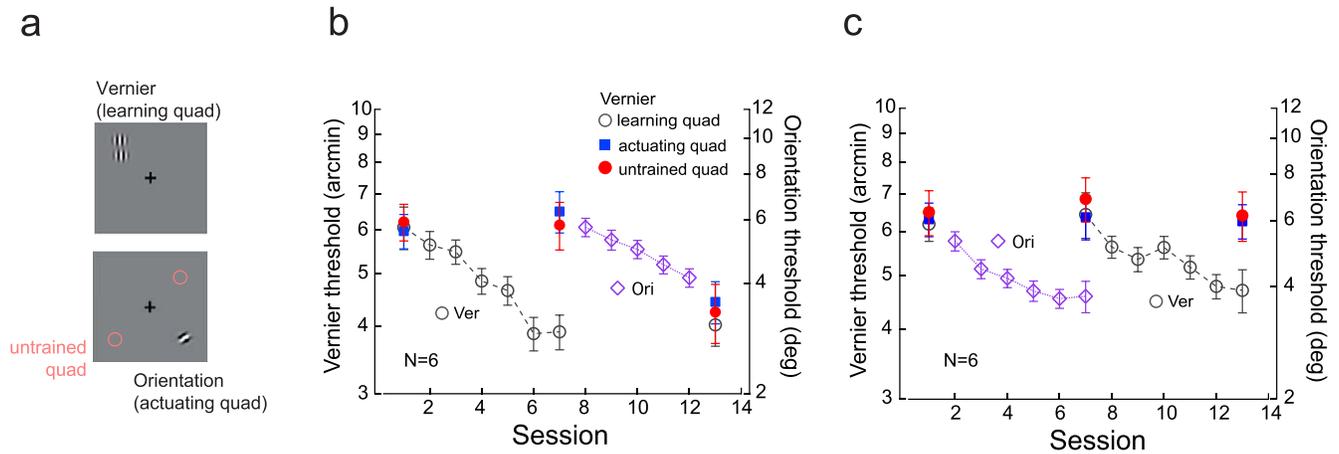


Figure 3. Sequential Vernier and actuator (orientation) trainings and the order effect. (a) Stimuli. The pink circles (not shown in actual stimuli) indicate the stimulus locations at the untrained quadrants. (b) Vernier alignment was first trained, and orientation discrimination as the actuator was then trained, in separate diagonal quadrants. The transfer of Vernier learning was tested at the actuating quadrant and untrained quadrants at the same 5° eccentricity. (c) The actuator (orientation) training preceded Vernier training in a reversed order. The transfer of Vernier learning was again tested at the actuating quadrant and the untrained quadrants at the same 5° eccentricity.

eccentricity (the “actuating quadrant,” Figure 1a). The secondary training tasks included motion direction, orientation, and contrast discrimination. This diagonal-quadrant spatial arrangement was identical to our original double-training condition in which Vernier learning was shown to transfer completely to a diagonal quadrant where an irrelevant task was trained (Wang et al., 2012). Thus, we expected that Vernier learning would transfer from the learning quadrant to the actuating quadrant with actuator training. However, in these new experiments we were particularly interested in whether Vernier learning would also transfer to other completely untrained retinal quadrants (“untrained quadrants,” Figure 1a).

Vernier learning by itself was highly location specific, with the transfer index (TI) = -0.10 ± 0.16 (calculated from Figure 3; also see Xiao et al., 2008; Wang et al., 2012), not significantly different from TI = 0 ($p_0 = 0.26$; p_0 and p_1 were p values when TIs were tested against TI = 0 and TI = 1, respectively). Vernier learning (MPI = $37.2 \pm 2.9\%$, $p < 0.001$, averaged over all 25 observers in Figure 1), when paired with direction learning (MPI = $31.6 \pm 6.4\%$, $p < 0.001$; Figure 1a), orientation learning (MPI = $41.0 \pm 8.4\%$, $p = 0.014$; Figure 1b), or contrast learning (MPI = $35.9 \pm 4.1\%$, $p = 0.006$; Figure 1c), transferred significantly to the actuating quadrant as expected. The mean Vernier improvement at the transfer location was $27.8 \pm 6.2\%$ ($p < 0.001$), $29.5 \pm 6.5\%$ ($p = 0.004$), and $21.7 \pm 4.6\%$ ($p = 0.004$), respectively. The corresponding TIs were 0.69 ± 0.15 ($p_1 = 0.022$), 0.61 ± 0.11 ($p_1 = 0.011$), and 0.87 ± 0.18 ($p_1 = 0.25$), suggesting partial or complete learning transfer.

Importantly, when paired with motion direction or orientation discrimination learning, Vernier learning

also transferred either partially or completely to a completely untrained quadrant either across the horizontal or vertical meridian (each measured in half the observers) at the same 5° retinal eccentricity (MPI = $20.1 \pm 7.0\%$, $p = 0.016$ and $35.9 \pm 7.4\%$, $p = 0.002$, respectively. MPIs were averaged over both quadrants). The corresponding TIs were 0.45 ± 0.18 ($p_1 = 0.003$) and 0.92 ± 0.20 ($p_1 = 0.69$), respectively. Vernier learning also transferred to a different 10° retinal eccentricity in one quadrant across the horizontal or vertical meridian (MPI = $31.6 \pm 8.8\%$, $p = 0.008$ and $28.4 \pm 6.6\%$, $p = 0.006$, respectively). Here the TI values were not applicable since the performance changes at two eccentricities were not comparable. However, when paired with contrast learning, there was no significant transfer of Vernier learning to untrained quadrants across the horizontal or vertical meridian at either 5° (MPI = $-0.5 \pm 10.7\%$, $p = 0.96$; TI = -0.12 ± 0.41 , $p_0 = 0.39$) or 10° (MPI = $5.5 \pm 5.2\%$, $p = 0.34$) retinal eccentricity. The transfer of Vernier learning paired with contrast learning was significantly less than that paired with motion direction learning and orientation learning ($t = 2.39$, $df = 22$, $p = 0.026$), confirming that there was a group-wise difference in the degree of transfer.

These striking differences of Vernier-learning transfer appeared to be linked to the transfer characteristics of the actuators. We measured the single-training transfer baselines of motion direction, orientation, and contrast-discrimination learning to the diagonal quadrant using identical stimulus configurations. The TIs of orientation and motion-direction learning were 0.85 ± 0.06 ($p_1 = 0.06$) and 0.77 ± 0.13 ($p_1 = 0.15$), respectively, suggesting that orientation and motion-direction learning were not very location specific under these condi-

tions. In contrast, the TI was 0.23 ± 0.12 ($p_0 = 0.13$) for contrast learning, suggesting that contrast learning was mainly location specific. The TIs of contrast-learning transfer were significantly lower than those of motion-direction and orientation learning ($t = 4.236$, $df = 14$, $p = 0.001$). Thus, Vernier learning might inherit the transfer characteristics of the actuators, so it transferred when paired with less location-specific orientation or motion-direction learning, but failed to do so when paired with more location-specific contrast learning.

Double training with learning and actuator at the same retinal location

In Figure 1 as well as in our previous double training studies (Xiao et al., 2008; Wang et al., 2012; Wang et al., 2013), Vernier learning and actuator training always took place at two separate locations. However, Figure 1 showed that the transfer of Vernier learning was enhanced when paired with less location-specific motion and orientation actuators. Thus, we reasoned that to the extent that motion and orientation actuators were less location specific, double training might not require training at two separate locations. To test this possibility, we repeated Figure 1 experiments with double training at the *same* retinal location. Specifically, Vernier training was paired with actuator training, either motion direction, orientation, or contrast-discrimination training, at the *same* retinal location at 5° retinal eccentricity.

When paired with direction learning (MPI = $37.3 \pm 3.5\%$, $p < 0.001$; Figure 2a) or orientation learning (MPI = $29.7 \pm 5.4\%$, $p = 0.002$; Figure 2b), Vernier learning (MPI = $29.9 \pm 3.0\%$, $p < 0.001$, averaged over all 18 observers in Figure 2) transferred completely to the untrained diagonal quadrant (MPI = $25.0 \pm 3.8\%$, $p < 0.001$, and $31.3 \pm 5.1\%$, $p < 0.001$, respectively). The corresponding TIs were 1.00 ± 0.20 ($p_1 = 0.50$) and 0.99 ± 0.19 ($p_1 = 0.48$), respectively. However, when paired with contrast learning (MPI = $29.5 \pm 5.2\%$, $p = 0.014$), no transfer of Vernier learning to the untrained quadrant was evident (MPI = $-6.8 \pm 12.9\%$, $p = 0.83$; TI = -0.22 ± 0.41 , $p_0 = 0.20$; Figure 1c). Here contrast learning and transfer were measured either with the two-Gabor stimuli using a single-interval 2AFC paradigm (Figure 2c-ii, as well as Figure 2c-iii with black and red bars; $n = 6$), or with a single Gabor target using a two-interval 2AFC paradigm (Figure 2c-iii with blue and pink bars; $n = 5$). Because in this study direction and orientation training always used two-interval 2AFC trials, here we added contrast training with two-interval 2AFC trials as a control. The control data indicate that the different actuating effects did not result from this methodological difference. As in Figure 1, the overall TIs of Vernier learning when paired with contrast learning were significantly lower than those

paired with motion-direction learning and orientation learning ($t = 3.63$, $df = 20$, $p = 0.002$).

Sequential double training and the effect of reversed order

One possible explanation for the broad transfer effects is that the temporal association between simultaneously trained location-specific Vernier and less location-specific actuator signals could potentially actuate the transfer of location-specific learning. Indeed similar temporal associations have been used to explain task irrelevant perceptual learning (Seitz & Watanabe, 2005). To examine this possibility, we studied the impact of sequential pairing of Vernier and orientation training on the transfer of Vernier learning (Figure 3a). Observers first practiced Vernier alignment at the learning quadrant for five sessions (MPI = $34.0 \pm 5.8\%$, $p = 0.002$), but learning did not transfer to the diagonal actuating quadrant (MPI = $-4.1 \pm 5.1\%$, $p = 0.46$; TI = -0.1 ± 0.16 , $p_0 = 0.26$), showing typical location specificity. The same observers then practiced orientation discrimination for another five sessions at the actuating quadrant (MPI = $25.7 \pm 3.7\%$, $p < 0.001$). After the less location-specific orientation learning, Vernier performance was improved at both the actuating quadrant (MPI = $26.9 \pm 1.3\%$, $p < 0.001$, TI = 0.98 ± 0.22 , $p_1 = 0.46$) and the untrained quadrants (MPI = $34.6 \pm 5.0\%$, $p < 0.001$, TI = 1.05 ± 0.21 , $p_1 = 0.41$, averaged from two untrained quadrants, each measured in half the observers). The high TI values indicate that the transfer of Vernier learning was complete. These sequential training data discounted temporal association as a potential mechanism for the broad transfer effects.

Importantly, when the order of the sequential training was reversed (Figure 3b), the initial orientation (actuator) learning (MPI = $27.8 \pm 1.4\%$, $p < 0.001$) had no impact on Vernier performance at the same actuating quadrant or other untrained quadrants (MPI = $-1.6 \pm 5.5\%$, $p = 0.78$). The subsequent Vernier learning at the learning quadrant (MPI = $30.6 \pm 3.8\%$, $p < 0.001$) also showed no transfer to the actuating quadrant and other untrained quadrants (overall MPI = $3.8 \pm 4.6\%$, $p = 0.44$ as compared to the pretraining performance). These data indicate that Vernier learning was actuated to transfer when the Vernier task was learned either before, or at the same time as, the actuator task, but not after the actuator learning.

Discussion

There are two novel findings in this study. First, the transfer of location-specific Vernier learning is depen-

dent on the transfer characteristics of the actuators: When paired with a less location-specific actuator (orientation or motion), Vernier learning transfers to completely untrained retinal locations. However, when paired with a more location-specific actuator (contrast discrimination), Vernier learning only transfers to the actuator-training location. Second, the transfer of Vernier learning can be equally enabled when Vernier and a less location-specific task are both trained at the same retinal location.

Overall the complete location transfer of perceptual learning revealed in our previous (Xiao et al., 2008; Wang et al., 2012; Wang et al., 2013) and current double training studies indicates that learning occurs in high-level brain areas beyond the retinotopic visual cortex. These location-transfer results challenge the claims that perceptual learning results from neuronal plasticity in the early visual cortex (Karni & Sagi, 1991; Fahle, 1994; Schoups et al., 1995; Crist et al., 1997; Bejjanki et al., 2011). The latter would predict at least partial location specificity of learning even with double training. The location transfer results, along with additional demonstrations of complete learning transfer to an orthogonal orientation (J. Y. Zhang et al., 2010) or an opposite motion direction (J. Y. Zhang & Yang, 2014), also challenge response reweighting theories (Mollon & Danilova, 1996; Doshier & Lu, 1999; Yu et al., 2004; Petrov, Doshier, & Lu, 2005). These theories propose that only the responses of the directly activated neurons are reweighted, so that reweighting-based learning predicts location and orientation specificity.

The current findings also challenge recent theories that have been specifically proposed to explain double training enabled learning transfer. Improved spatial attention (Xiao et al., 2008), off-task self-organization of top-down connections (Solgi et al., 2013), or up-regulation of location-independent weights due to double training (Liu et al., 2011) may account for Vernier-learning transfer to a different actuating location. However, these mechanisms may not explain why learning transfers to other completely untrained locations, especially when double training are performed at the same retinal location, and why in these cases the learning transfer depends on the transfer characteristics of the actuator learning.

Perceptual-learning research traditionally emphasizes that learning is specific. For example, learning of various visual tasks used in the current study, including Vernier, contrast, orientation, and motion-direction learning are reported to be location specific in early studies (Ball & Sekuler, 1987; Shiu & Pashler, 1992; Schoups et al., 1995; Fahle, 1997; Yu et al., 2004). However, our single-condition baseline training shows that peripheral orientation and motion-direction learning both transfer significantly to other untrained

locations, consistent with recent reports (e.g., Jeter et al., 2009; T. Zhang, Xiao, Klein, Levi, & Yu, 2010; E. Zhang, Zhang, & Li, 2013; Hung & Seitz, 2014). On the other hand, contrast and Vernier learning is still largely location specific without double training. We have hypothesized that learning transfer to a new location depends on whether high-level learning can functionally connect to the new location. This hypothesis is supported by our ERP evidence that learning transfer is associated with top-down modulation of the P1 and N1 components, and even the C1 component, when the trained task is performed at the transfer location (G. L. Zhang, Cong, Song, & Yu, 2013a, 2013b). Orientation and motion-direction training appears to activate a global process that connects high-level learning not only to the trained location, but also to untrained locations. This connection is absent in Vernier and contrast training without double training. Why the top-down connection from high-level learning to untrained locations in single-condition training is task specific is as yet unknown. We suspect that feature attention may play a role because attention to orientation and motion direction can activate similarly tuned neurons in other spatially unattended locations through frontal feedback (McAdams & Maunsell, 2000; Martinez-Trujillo & Treue, 2004; Cohen & Maunsell, 2011). New experiments are required to study the precise mechanisms underlying this task-specific effect.

Why is the transfer of Vernier learning dependent on the transfer characteristics of actuator learning? It appears that when paired with less location-specific actuators (i.e., orientation or motion direction), Vernier learning is “piggybacked” to new locations via the latter’s global connections. Again, the exact mechanisms underlying this piggybacking process are unknown. The same global connections may not be available when the actuator is the more location-specific contrast learning. In this case Vernier learning can only transfer to a different actuator location (Figure 1c) where high-level learning connects to neurons at the actuator location that are potentiated by contrast training, but not to other untrained quadrants.

Hung and Seitz (2014) recently replicated our piggybacking results originally reported as a conference abstract (J. Y. Zhang et al., 2012). They report that Vernier-learning transfer can be actuated by orientation learning at the same location, but only when Vernier training was performed with multiple short staircases as in our experiments. There was no learning transfer when the Vernier task was practiced with a single long staircase through each entire session. Hung and Seitz attributed this effect to the fact that a single long staircase exposes observers to a greater proportion of difficult trials. We will discuss Hung and Seitz’s results in detail elsewhere.

In summary, our results show that Vernier learning, previously thought to be highly location specific, can be piggybacked to completely untrained retinal locations, when paired with orientation or motion-direction learning, but not with contrast learning. The mechanisms underlying this task-specific piggybacking effect are unknown. We hope that our results will attract new studies that would bring new insights into the understanding of perceptual learning. We also hope that the new training paradigms reported in this study will help guide the development of more efficient protocols for clinical visual training and rehabilitation.

Keywords: perceptual learning, transfer, double training, Vernier

Acknowledgments

This research was supported by the Natural Science Foundation of China Grants 31230030 (CY) and 31470975 (JYZ), and by the US National Institute of Health Grants RO1EY01728 and RO1EY 04776 (DML & SAK). We thank Wu Li, Zhonglin Lu, and Aaron Seitz for their helpful comments during the preparation of this manuscript.

*RW and J-YZ contributed equally to this work.
Commercial relationships: none.
Corresponding authors: Cong Yu; Jun-Yun Zhang.
Email: yucong@pku.edu.cn; zhangjunyun@pku.edu.cn.
Address: Department of Psychology, Peking University, Beijing, China.

References

- Ahissar, M., & Hochstein, S. (1997). Task difficulty and the specificity of perceptual learning. *Nature*, 387(6631), 401–406.
- Ball, K., & Sekuler, R. (1987). Direction-specific improvement in motion discrimination. *Vision Research*, 27(6), 953–965.
- Bejjanki, V. R., Beck, J. M., Lu, Z. L., & Pouget, A. (2011). Perceptual learning as improved probabilistic inference in early sensory areas. *Nature Neuroscience*, 14(5), 642–648.
- Cohen, M. R., & Maunsell, J. H. (2011). Using neuronal populations to study the mechanisms underlying spatial and feature attention. *Neuron*, 70(6), 1192–1204.
- 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.
- Dosher, B. A., Jeter, P., Liu, J., & Lu, Z. L. (2013). An integrated reweighting theory of perceptual learning. *Proceedings of the National Academy of Sciences, U S A*, 110(33), 13678–13683.
- Dosher, B. A., & Lu, Z. L. (1999). Mechanisms of perceptual learning. *Vision Research*, 39(19), 3197–3221.
- Fahle, M. (1994). Human pattern recognition: Parallel processing and perceptual learning. *Perception*, 23(4), 411–427.
- Fahle, M. (1997). Specificity of learning curvature, orientation, and vernier discriminations. *Vision Research*, 37, 1885–1895.
- Hung, S. C., & Seitz, A. R. (2014). Prolonged training at threshold promotes robust retinotopic specificity in perceptual learning. *Journal of Neuroscience*, 34(25), 8423–8431.
- Jeter, P. E., Dosher, B. A., Petrov, A., & Lu, Z. L. (2009). Task precision determines specificity of perceptual learning. *Journal of Vision*, 9(3):1, 1–13, <http://www.journalofvision.org/content/9/3/1>, doi: 10.1167/9.3.1. [PubMed] [Article]
- 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, U S A*, 88(11), 4966–4970.
- Liu, J., Lu, Z. L., & Dosher, B. (2011). Multi-location augmented hebbian reweighting accounts for transfer of perceptual learning following double training. *Journal of Vision*, 11(11): 992, <http://www.journalofvision.org/content/11/11/992>, doi:10.1167/11.11.992. [Abstract]
- Martinez-Trujillo, J. C., & Treue, S. (2004). Feature-based attention increases the selectivity of population responses in primate visual cortex. *Current Biology*, 14(9), 744–751.
- McAdams, C. J., & Maunsell, J. H. (2000). Attention to both space and feature modulates neuronal responses in macaque area V4. *Journal of Neurophysiology*, 83(3), 1751–1755.
- Mollon, J. D., & Danilova, M. V. (1996). Three remarks on perceptual learning. *Spatial Vision*, 10(1), 51–58.
- Petrov, A. A., Dosher, B. A., & Lu, Z. L. (2005). The dynamics of perceptual learning: An incremental reweighting model. *Psychological Review*, 112(4), 715–743.

- Schoups, A., Vogels, R., & Orban, G. A. (1995). Human perceptual learning in identifying the oblique orientation: Retinotopy, orientation specificity and monocularly. *Journal of Physiology*, *483*(Pt 3), 797–810.
- Seitz, A., & Watanabe, T. (2005). A unified model for perceptual learning. *Trends in Cognitive Sciences*, *9*(7), 329–334.
- Shiu, L. P., & Pashler, H. (1992). Improvement in line orientation discrimination is retinally local but dependent on cognitive set. *Perception & Psychophysics*, *52*(5), 582–588.
- Solgi, M., Liu, T., & Weng, J. (2013). A computational developmental model for specificity and transfer in perceptual learning. *Journal of Vision*, *13*(1):7, 1–23, <http://www.journalofvision.org/content/13/1/7>, doi:10.1167/13.1.7. [PubMed] [Article]
- Wang, R., Cong, L. J., & Yu, C. (2013). The classical TDT perceptual learning is mostly temporal learning. *Journal of Vision*, *13*(5):9, 1–9, <http://www.journalofvision.org/content/13/5/9>, doi:10.1167/13.5.9. [PubMed] [Article]
- 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.
- 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. *Current Biology*, *18*(24), 1922–1926.
- Yu, C., Klein, S. A., & Levi, D. M. (2004). Perceptual learning in contrast discrimination and the (minimal) role of context. *Journal of Vision*, *4*(3):4, 169–182, <http://www.journalofvision.org/content/4/3/4>, doi:10.1167/4.3.4. [PubMed] [Article]
- Zhang, E., Zhang, G. L., & Li, W. (2013). Spatiotopic perceptual learning mediated by retinotopic processing and attentional remapping. *European Journal of Neuroscience*, *38*(12), 3758–3767.
- Zhang, G. L., Cong, L. J., Song, Y., & Yu, C. (2013a). ERP C1 changes associated with transfer of perceptual learning at an untrained retinal location. *Journal of Vision*, *13*(9): 909, <http://www.journalofvision.org/content/13/9/909>, doi:10.1167/13.9.909. [Abstract]
- Zhang, G. L., Cong, L. J., Song, Y., & Yu, C. (2013b). ERP P1-N1 changes associated with Vernier perceptual learning and its location specificity and transfer. *Journal of Vision*, *13*(4):19, 1–13, <http://www.journalofvision.org/content/13/4/19>, doi:10.1167/13.4.19. [PubMed] [Article]
- Zhang, J. Y., Cong, L. J., Klein, S. A., Levi, D. M., & Yu, C. (2014). Perceptual learning improves adult amblyopic vision through rule-based cognitive compensation. *Investigative Ophthalmology & Visual Science*, *55*(4), 2020–2030, <http://www.iovs.org/content/55/4/2020>. [PubMed] [Article]
- Zhang, J. Y., Wang, R., Klein, S. A., Levi, D. M., & Yu, C. (2012). Perceptual learning transfers to untrained retinal locations after double training: A piggyback effect. *Journal of Vision*, *12*(9): 1026, <http://www.journalofvision.org/content/12/9/1026>, doi:10.1167/12.9.1026. [Abstract]
- Zhang, J. Y., & Yang, Y. X. (2014). Perception learning of motion direction discrimination transfers to an opposite direction with TPE training. *Vision Research*, *99*, 93–98.
- Zhang, J. Y., Zhang, G. L., Xiao, L. Q., Klein, S. A., Levi, D. M., & Yu, C. (2010). Rule-based learning explains visual perceptual learning and its specificity and transfer. *Journal of Neuroscience*, *30*(37), 12323–12328.
- Zhang, T., Xiao, L. Q., Klein, S. A., Levi, D. M., & Yu, C. (2010). Decoupling location specificity from perceptual learning of orientation discrimination. *Vision Research*, *50*(4), 368–374.