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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

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could reweight the responses of various activated sensory neurons to improve decision making (Mollon & Danilova, 1996; Dosher & 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, Dosher, 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, Dosher 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 (Dosher, 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, & Dosher, 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.

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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/m^2. 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.

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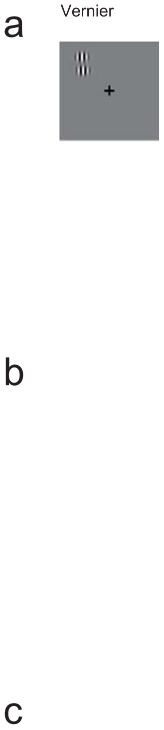
The Vernier stimulus consisted of a pair of identical Gabors (Gaussian-windowed sinusoidal gratings) on a mean luminance screen background, which was centered in one retinal quadrant (Figure 1a). The two



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 $0.47 + \Delta C$. 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

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 + Δdirection) 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 + Δorientation) 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.

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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.

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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

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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

tions. In contrast, the TI was 0.23 ± 0.12 ($_0 = 0.13$) 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 ($t = 4.236$, $df = 14$, $= 0.001$). 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.

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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 ± 3.5%, < 0.001; Figure 2a) or orientation learning (MPI = 29.7 ± 5.4%, $= 0.002$; Figure 2b), Vernier learning (MPI = 29.9 ± 3.0%, < 0.001, averaged over all 18 observers in Figure 2) transferred completely to the untrained diagonal quadrant (MPI = 25.0 ± 3.8%, < 0.001, and 31.3 ± 5.1%, < 0.001, respectively). The corresponding TIs were 1.00 ± 0.20 ($_1 = 0.50$) and 0.99 ± 0.19 ($_1 = 0.48$), respectively. However, when paired with contrast learning (MPI = 29.5 ± 5.2%, $= 0.014$), no transfer of Vernier learning to the untrained quadrant was evident (MPI = −6.8 ± 12.9%, $= 0.83$; TI = −0.22 ± 0.41, $_0 = 0.20$; 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; $= 6$), or with a single Gabor target using a two-interval 2AFC paradigm (Figure 2c-iii with blue and pink bars; $= 5$). 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 ($t = 3.63$, $df = 20$, $= 0.002$).

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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 ± 5.8%, $= 0.002$), but learning did not transfer to the diagonal actuating quadrant (MPI = −4.1 ± 5.1%, $= 0.46$; TI = −0.1 ± 0.16, $_0 = 0.26$), showing typical location specificity. The same observers then practiced orientation discrimination for another five sessions at the actuating quadrant (MPI = 25.7 ± 3.7%, < 0.001). After the less location-specific orientation learning, Vernier performance was improved at both the actuating quadrant (MPI = 26.9 ± 1.3%, < 0.001, TI = 0.98 ± 0.22, $_1 = 0.46$) and the untrained quadrants (MPI = 34.6 ± 5.0%, < 0.001, TI = 1.05 ± 0.21, $_1 = 0.41$, 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 ± 1.4%, < 0.001) had no impact on Vernier performance at the same actuating quadrant or other untrained quadrants (MPI = −1.6 ± 5.5%, $= 0.78$). The subsequent Vernier learning at the learning quadrant (MPI = 30.6 ± 3.8%, < 0.001) also showed no transfer to the actuating quadrant and other untrained quadrants (overall MPI = 3.8 ± 4.6%, $= 0.44$ 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.

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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; Dosher & Lu, 1999; Yu et al., 2004; Petrov, Dosher, & 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 [illegible]

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

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