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Report

Complete Transfer of Perceptual Learning across Retinal Locations Enabled by Double Training

Lu-Qi Xiao,[1,3] Jun-Yun Zhang,[1,3] Rui Wang,[1]
Stanley A. Klein,[2] Dennis M. Levi,[2] and Cong Yu[1,*]
[1]State Key Laboratory of Cognitive Neuroscience
and Learning
Beijing Normal University
Beijing 100875
China
[2]School of Optometry and Helen Wills Neuroscience Institute
University of California
Berkeley, CA 94720
USA

Summary

Practice improves discrimination of many basic visual features, such as contrast, orientation, and positional offset [1–7]. Perceptual learning of many of these tasks is found to be retinal location specific, in that learning transfers little to an untrained retinal location [1, 6–8]. In most perceptual learning models, this location specificity is interpreted as a pointer to a retinotopic early visual cortical locus of learning [1, 6–11]. Alternatively, an untested hypothesis is that learning could occur in a central site, but it consists of two separate aspects: learning to discriminate a specific stimulus feature ("feature learning"), and learning to deal with stimulus-nonspecific factors like local noise at the stimulus location ("location learning") [12]. Therefore, learning is not transferable to a new location that has never been location trained. To test this hypothesis, we developed a novel double-training paradigm that employed conventional feature training (e.g., contrast) at one location, and additional training with an irrelevant feature/task (e.g., orientation) at a second location, either simultaneously or at a different time. Our results showed that this additional location training enabled a complete transfer of feature learning (e.g., contrast) to the second location. This finding challenges location specificity and its inferred cortical retinotopy as central concepts to many perceptual-learning models and suggests that perceptual learning involves higher nonretinotopic brain areas that enable location transfer.

Results

We first replicated the common finding of location specificity in a conventional perceptual-learning paradigm. Observers practiced contrast discrimination (i.e., "which interval contained a higher contrast stimulus in a two-interval trial?") for a vertical (V)-Gabor patch (Figure 1A) located 5° from fixation in the lower left or upper left quadrant of the visual field (denoted as "ctrst-loc1," contrast discrimination at location 1; Figure 1B). Significant learning was evident at loc1 after five to six 2 hr sessions of practice with one session per day in eight observers (Figures 1B and 1D; mean % improvement [MPI] = 24.6 ± 2.7, $p < 0.001$, paired t test). However, contrast discrimination did not improve significantly for the same stimulus at an untrained location symmetrically across the horizontal meridian of the visual field (ctrst-loc2) (Figures 1B and 1D; MPI = 5.7 ± 3.4, $p = 0.102$).

We created a novel double-training paradigm to test whether location specificity results from a lack of training of factors unspecific to the stimulus feature at the untrained transfer location. In the paradigm, observers underwent conventional feature training for discrimination of a specific stimulus feature at one retinal location. In addition, they received location training at another location (referred to as the transfer location because the transfer of feature learning would be tested here) with an irrelevant stimulus feature and task. Five new observers practiced the feature training task (contrast discrimination for the V-Gabor at loc1 [ctrst-loc1]) and the location training task with a completely different feature and task (orientation discrimination for a horizontal [H]-Gabor at loc2 [ori-loc2]) in alternating blocks of trials. The H-Gabor contrast was jittered from 0.30 to 0.67 for every single presentation to minimize any potential contrast learning at loc2 during location training. After practice, performance for ctrst-loc1 and ori-loc2 both improved significantly (Figure 1C; MPI = 30.1 ± 4.8, $p = 0.003$ for ctrst-loc1; MPI = 30.6 ± 4.9, $p = 0.003$ for ori-loc2). Most importantly, contrast discrimination for the V-Gabor at loc2 (ctrst-loc2) also improved significantly (Figure 1C; MPI = 32.4 ± 2.5, $p < 0.001$), by as much as the improvement for trained ctrst-loc1 ($p = 0.395$). Assuming equal impact of location training at loc1 and loc2, these results suggest complete transfer of feature learning as a result of doubling training, which is in sharp contrast to the nonsignificant performance change in conventional training (Figures 1B and 1D).

To evaluate the separate contributions of feature and location training and their potential interactions, six new observers performed a sequential double-training task in which location training preceded feature training. Initial location training with H-Gabor orientation discrimination at loc2 (ori-loc2) (Figure 2; MPI = 38.3 ± 5.5, $p = 0.001$) improved V-Gabor contrast discrimination at the same location in all six observers (ctrst-loc2) (Figure 2; MPI = 15.9 ± 4.2, $p = 0.013$; this location-training-induced improvement was not shown in Vernier learning, see Figure 3 below). Moreover, successive feature training with V-Gabor contrast discrimination at loc1 (ctrst-loc1) (Figure 2; MPI = 27.9 ± 3.7, $p = 0.001$) resulted in further significant improvement in ctrst-loc2 in five out of six observers (Figure 2; MPI = 19.2 ± 6.0, $p = 0.024$, over and above the initial-training-induced performance changes). This improvement was in contrast to nonsignificant transfer in conventional training, which was identical except without prior location training (gray bar in Figure 2C, replotted from Figure 1D). The overall improvement in ctrst-loc2 after two stages of training was 32.1% (Figure 2C), comparable to the outcome of feature training (27.9%, Figure 2C) for ctrst-loc1 ($p = 0.337$). Again, assuming equal impact of location learning at both locations, feature learning at loc1 transferred completely to loc2 after location training.

These results suggest that location training may have primed the trained location, which enabled stimulus feature

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*Correspondence: yucong@bnu.edu.cn
[3]These authors contributed equally to this work

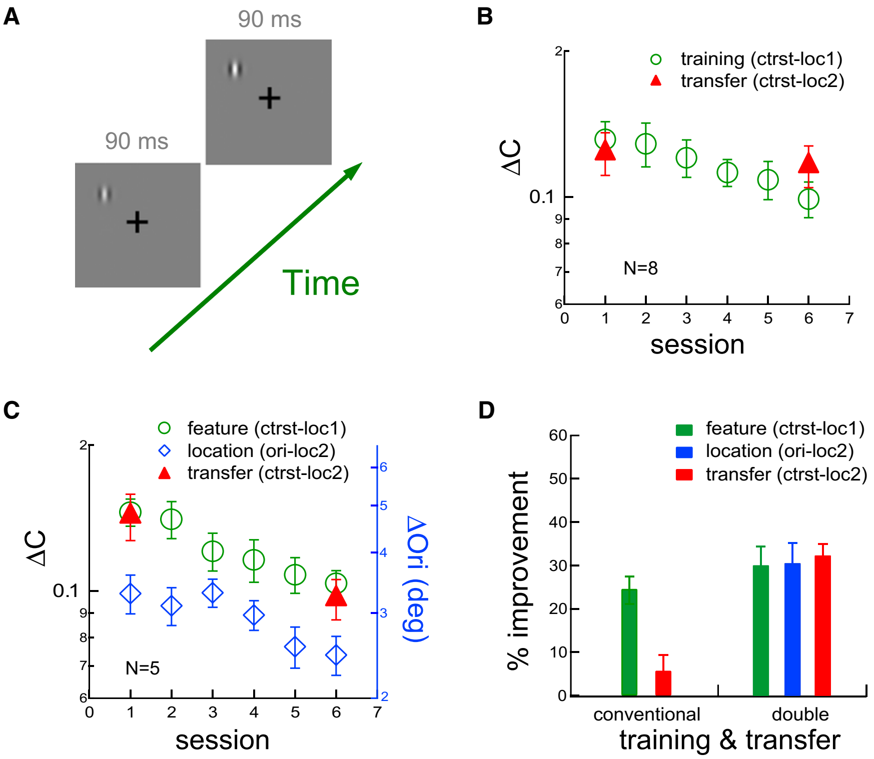

Figure 1. Retinal Location Specificity Studied with the Conventional and Double-Training Paradigms

(A) The stimulus configuration in a 2AFC trial in this figure and Figure 2 experiments. One interval contains a higher-contrast Gabor stimulus (Gaussian windowed sinusoidal grating).

(B) Conventional training. Contrast discrimination for a V-Gabor was practiced at loc1 (ctrst-loc1, green circles) and its transfer was tested at loc2 (ctrst-loc2, red triangles). Data are pooled from all participating observers, and error bars represent one standard error of the mean.

(C) Double training. Contrast discrimination was practiced at loc1 as feature training (ctrst-loc1, green circles; contrast thresholds indicated by the left ordinate), and orientation discrimination for a H-Gabor was practiced at loc2 as additional location training (ori-loc2, blue diamonds; orientation thresholds indicated by the right ordinate), in alternating blocks of trials (staircases). The transfer was tested for V-Gabor contrast discrimination at loc2 (ctrst-loc2; red triangles). The left and right ordinates have the identical scale factor in log units.

(D) A summary of training results as well as the resultant transfers as percent improvement with conventional and double training.

learning at other locations to transfer over. To test the generality of this finding, we replicated the doubling-training results in a Vernier discrimination task (Figure 3A) with a more efficient design.

Five observers first practiced Vernier discrimination in six 2 hr sessions with one session per day. The stimulus was either horizontally or vertically oriented and presented in either the upper left or lower left quadrant of the visual field during training and pre- and post-training testing. In the first phase of the experiment, practice produced significant learning at the trained orientation and quadrant (ori1_loc1) (Figures 3B and 3C, blue diamonds; MPI = 22.0 ± 4.4, $p = 0.002$). However, this learning did not transfer to the untrained quadrant (ori1_loc2, first two purple squares; MPI = −8.2 ± 5.5, $p = 0.335$). Neither did it transfer to the orthogonal orientation at the same trained location (ori2_loc1, first two red triangles; MPI = 0.0 ± 7.7, $p = 0.997$). These results confirmed the well-known location and orientation specificities of Vernier and hyperacuity learning in the conventional learning paradigm [5].

In the context of double training, here the observers were performing two parallel sets of successive double training. Practice at ori1_loc1 in the first set of double training could be regarded as feature training for target stimulus ori1_loc2 (same orientation, secondary location), and in the second set could be regarded as location training for another target stimulus ori2_loc1 (orthogonal orientation, same location). In the next phase of double training, the observers practiced Vernier discrimination for an orthogonal orientation at a secondary location (ori2_loc2). This new training served as successive location training for target stimulus ori1_loc2 in the first set of double training, and as successive feature training for another target stimulus ori2_loc1 in the second set of double training.

Our results showed that, after successive location training (ori2_loc2) (Figures 3B and 3C, green circles; MPI = 27.2 ± 4.8, $p = 0.003$), performance for the target stimulus ori1_loc2 was now improved significantly (the second and third purple squares; MPI = 24.7 ± 4.0, $p = 0.004$, over and above the initial training-induced performance changes). This result confirmed that location training, even after feature learning, triggered the location transfer of earlier feature learning (ori1_loc1). The MPIs for feature-trained ori1_loc1 and feature-untrained but location-trained target stimulus ori1_loc2 were 22.0% and 24.7%, respectively (Figure 3D, the blue bar and the right purple bar; $p = 0.552$), showing complete transfer of feature learning across retinal locations after double training.

Moreover, the same secondary training at ori2_loc2 as successive feature learning also transferred significantly to a secondary location (ori2_loc1) (the second and third red triangles; MPI = 20.7 ± 4.0, $p = 0.001$, over and above the initial training-induced performance changes) after earlier location training at ori1_loc1. The MPIs for feature-trained ori2_loc2 and feature-untrained but location-trained target stimulus ori2_loc1 were 27.3% and 20.7%, respectively (Figure 3D, the green bar and the right red bar; $p = 0.287$), so the transfer of feature learning from loc2 to loc1 was again nearly complete after double training. In both sets of double training, the degrees of learning and transfer were highly correlated ($r = 0.96$). Observers who improved most at trained ori1_loc1 and ori2_loc2 showed the largest improvement at untrained target stimuli ori2_loc1 and ori1_loc2.

In general, results from these two sets of double training are in line with earlier double-training results in contrast learning tasks. Therefore, complete transfer of feature learning enabled by location training appears to be a general effect.

Discussion

Single-unit and fMRI studies have shown that not only the retinotopic early visual cortex, but also the nonretinotopic higher brain areas that are more related to attention and decision

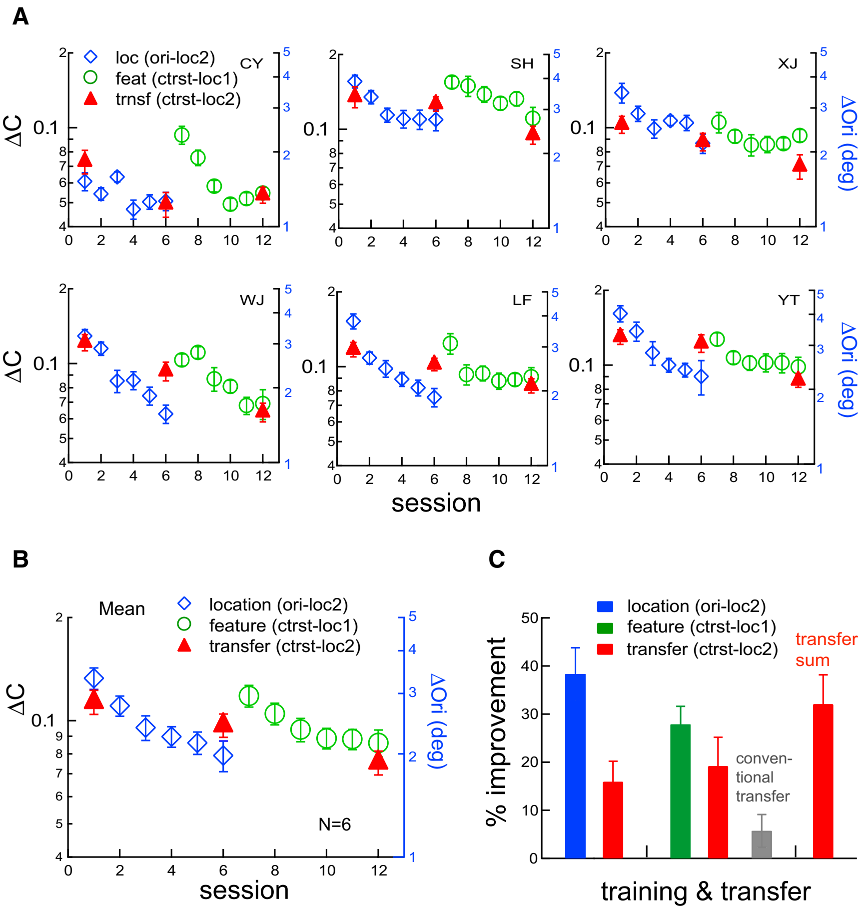

Figure 2. Sequential Double Training

(A and B) Individual and mean plots. H-Gabor orientation discrimination was first practiced at loc2 as location learning (ori-loc2, blue diamonds; orientation thresholds indicated by the right ordinate), and its transfer to V-Gabor contrast discrimination at the same loc2 was tested (ctrst-loc2, first two red triangles; contrast thresholds indicated by the left ordinate). Then V-Gabor contrast discrimination at loc1 was practiced as feature training (ctrst-loc1, green circles), and its transfer to ctrst-loc2 was tested (the second and third red triangles). This part of training was identical to conventional training in Figure 1B. The right and left ordinates have the identical scale factor in log units.

(C) A summary of initial location learning and its transfer (left blue and red bars), successive feature learning and its transfer (middle green and red bars; the gray bar replotted from Figure 1D indicates conventional learning transfer), and the overall transfer (right red bar) as percent improvement.

making, are involved in visual discrimination [13, 14]. However, most studies on the neural mechanisms of perceptual learning have focused on response changes in the retinotopic early visual cortex [9, 15–18], as motivated by the often observed strict location specificity and the inferred retinotopy. The complete transfer of perceptual learning to new retinal locations revealed by double training calls into question both location specificity as a key property of visual perceptual learning and the well-received belief by many researchers that the retinotopic early visual cortex is the neuronal basis of perceptual learning. Rather, it points to a crucial role for nonretinotopic higher brain areas that engage attention and decision making for perceptual learning.

The complete transfer of learning across retinal locations challenges many existing perceptual-learning models that are more or less constrained by location specificity. For example, Adini, Tsodyks, and Sagi [19] modeled perceptual learning as training-induced modification of recurrent connections in V1. This model would not predict transfer of learning to other retinal locations without incorporating learning in higher brain areas. At the post-V1 level, the Lu and Dosher model [20, 21] suggests training-induced reweighting of V1 neuronal responses. Such response reweighting, as our data suggest, would have to at least partially occur in nonretinotopic areas, so that the model would allow location transfer of learning. Apparently our results are more consistent with Mollon and Danilova's hypothesis [12] that feature learning could take place in a more central site, but is not transferable to a new location because of the local noise at the new location. Another possibility is that learning could occur in both central and peripheral sites, which would be consistent with all current models and not necessarily contradictory to our data. However, the latter hypothesis is less favored by recent evidence that motion-direction learning is correlated with activity changes in a decision area LIP, but not the sensory area MT [22], and that orientation learning is more correlated to changes in V4, rather than V1, neurons [23, 24]. For orientation learning, even orientation tuning changes in V4 neurons are too small to fully account for behavioral orientation learning [23]. Therefore, brain areas higher than V4 must have involved. This is consistent with recent fMRI evidence [13] that high brain areas, including the intraparietal sulcus, frontal eye field, and supplementary eye field, participate in visual perceptual learning.

As an extension of the Mollon and Danilova hypothesis, our results further demonstrate that central learning can guide visual discrimination at a new location, provided that the new location has been primed by location training. Figure 2 shows that contrast learning transfers from loc1 to loc2 after orientation training at loc2, suggesting that location learning is stimulus feature/task nonspecific. We hypothesize that location learning improves spatial attention, which is stimulus nonspecific, to a peripheral location. Such improvement may be necessary because our everyday experience is probably insufficient as location training in the visual periphery for demanding visual discrimination tasks near their thresholds. There is evidence that spatial attention excludes unwanted noise without affecting the stimulus template [25]. If the stimulus template learned through feature training is stored in a central site, it would now be able to respond to the same stimulus at a new retinal location where noise has been excluded through location training.

Many perceptual learning studies including ours involve discrimination of basic simple stimulus features like orientation, contrast, etc. Retinal location specificity is central to many models proposing that perceptual learning of this kind relies on unique mechanisms largely based on sensory cortex and does not involve general mechanisms such as those involved in associative learning [26]. In addition, there are studies that

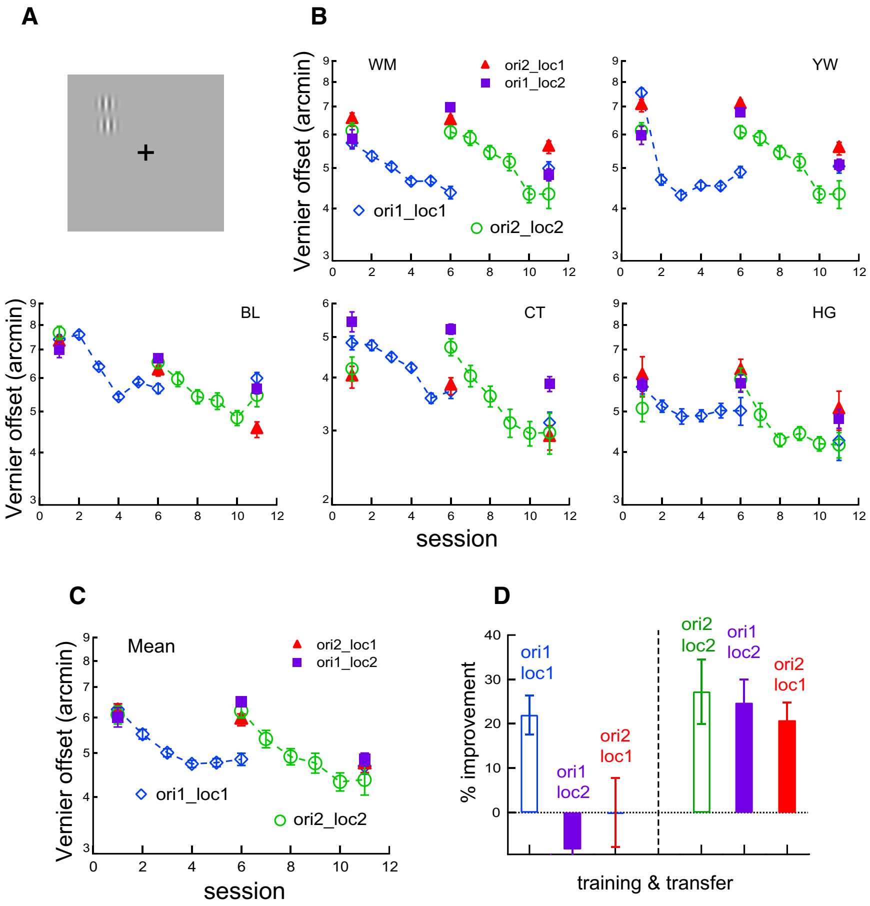

Figure 3. Sequential Double Training for Vernier Discrimination

(A) The stimulus configuration. The Vernier stimulus was presented at either the horizontal or vertical orientation, and in either the lower left or upper left visual quadrant.

(B and C) Individual and mean plots. Vernier discrimination was practiced at ori1_loc1 (blue open diamonds), and its transfer to a different quadrant (ori1_loc2, the first two purple squares) and to the orthogonal orientation at the same quadrant (ori2_loc1, the first two red triangles) were measured to show conventional location and orientation specificity in Vernier learning. In a double-training context, for the target stimulus ori2_loc1 (red triangles), initial practice at ori1_loc1 (blue diamonds) served as location training, and the later practice at ori2_loc2 (green circles) served as feature training. This double training resulted in nearly complete transfer of learning to the target stimulus ori2_loc1 (last two red triangles). In parallel, for another target stimulus ori1_loc2, initial practice at ori1_loc1 also served as feature training, and the later practice at ori2_loc2 (green circles) served as location training. Again this double training resulted in complete transfer of feature learning to target stimulus ori1_loc2 (last two purple squares).

(D) A summary of initial (feature or location) learning at ori1_loc1 and its transfers to target stimuli ori1_loc2 and ori2_loc1 (the left three bars) and later (location or feature) training at ori2_loc2 and its additional transfers to target stimuli ori1_loc2 and ori2_loc1 (right three bars).

use more complex stimuli to investigate the roles of more general processes in perceptual learning [27, 28]. Complex stimuli are typically not presented in a single retinal location, so their learning is presumably nonspecific to retinal locations and occurs in higher brain areas. By demonstrating complete location transfer of perceptual learning of basic visual features, we argue that higher brain areas are also critically involved in basic visual feature learning. Therefore, it is likely that at least partially overlapping mechanisms in higher brain areas could contribute to perceptual learning of both basic and more complex stimuli.

Experimental Procedures

Observers and Apparatus

Twenty-two observers with normal or corrected-to-normal vision participated in different experiments of this study. All were new to psychophysical experiments and unaware of the purposes of the study.

The stimuli were generated by a PC-based WinVis program (Neurometrics Institute, Oakland, CA). Gabor stimuli were presented on a 21-inch Sony G520 color monitor (1024 pixel × 768 pixel, 0.37 mm [H] × 0.37 mm [V] per pixel, 120 Hz frame rate, and 50 cd/m^2 mean luminance for contrast and orientation learning experiments; and 2048 pixel × 1536 pixel, 0.19 mm [H] × 0.19 mm [V] per pixel, 75 Hz frame rate, 50 cd/m^2 mean luminance for vernier learning experiments). The luminance of the monitor was linearized by an 8-bit look-up table. Viewing was monocular with one eye covered with a translucent plastic pad. A chin-and-head rest helped stabilize the head of the observer. Experiments were run in a dimly lit room.

Stimuli

For contrast-discrimination tasks, the test stimulus was a Gaussian windowed sinusoidal grating (Gabor) on a mean luminance screen background and presented in the upper left or lower left visual quadrant at 5° retinal eccentricity (Figure 1A). The stimulus contrast were defined as $(L_{max} - L_{min})/(L_{max} + L_{min})$, where L_{max} was the maximal luminance and L_{min} was the minimal luminance of the stimuli (i.e., Michelson contrast). The spatial frequency of the Gabor stimuli was 1.5 cycles per degree (cpd), the standard deviation of the Gaussian envelope was equal to the wavelength (λ) of the sinusoidal carrier, and the base contrast was 0.45. The viewing distance was 1 m. The same Gabor stimuli were also used for orientation discrimination training (Figures 1C and 2) with contrast jittered from 0.30 to 0.67. When orientation discrimination was performed, stimuli were viewed through a circular opening (diameter = 170°) of a black cardboard that covered the entire monitor screen. This control prevented observers from using external references to determine the orientations of the stimuli.

For Vernier discrimination tasks, the test stimulus was formed by a pair of identical Gabors on a mean luminance screen background and presented in the upper left or lower left visual quadrant at 5° retinal eccentricity (Figure 3A). The two Gabors had the same spatial frequency (3 cpd), standard deviation (2λ), contrast (0.45), and orientation (vertical or horizontal), and had a center-to-center distance of 4λ. The position of each Gabor shifted half the Vernier offset in opposite directions perpendicular to the Gabor orientation. The viewing distance was 1.5 m.

Procedure

Contrast and orientation discrimination thresholds were measured with a temporal 2AFC staircase procedure. In each trial, the test and reference stimuli were separately presented in two 92 ms stimulus intervals in a random order separated by a 600 ms interstimulus interval. The observer's task was to judge which stimulus interval contained the stimulus at a higher contrast (contrast discrimination) or at a more clockwise orientation (orientation discrimination). A small fixation cross preceded each trial by 400 ms and stayed through the trial.

Vernier discrimination thresholds were measured with a single-trial 2AFC staircase procedure. In each trial, the Vernier stimulus was presented for 92 ms. The observer's task was to judge whether the right Gabor was higher or lower than the left Gabor for a horizontal Vernier stimulus, or the lower Gabor was to the left or right of the upper Gabor for a vertical Vernier stimulus.

A small fixation cross preceded each trial by 400 ms and stayed through the trial.

Auditory feedback was given on incorrect responses. The step size of the staircase was 0.05 log units. A classical 3-down-1-up staircase rule was used, which resulted in a 79.4% convergence rate. Each staircase consisted of four preliminary reversals and six experimental reversals. The geometric mean of the experimental reversals was taken as the threshold for each staircase run.

Eye Movement

We used an Eyelink II eye tracker to assess the impact of eye movement. Five new observers performed an orientation-discrimination task identical to the one in Figure 1C for 3–5 sessions. During the first interval, the eye positions on the average were within 0.5° and 1° from the fixation in 90.3% and 98.9% of the trials, respectively, similar to those in a fixation-only control condition ($p = 0.29$ and 0.37, respectively). Therefore, Figure 3 data for single-interval Vernier learning were unaffected by eye movement. Moreover, the eye positions in the second interval were within 0.5° and 1° from the fixation in 78.3% and 96.1% of the trials, respectively, suggesting some mainly within 0.5° involuntary eye drifts. However, practice did not reduce the second-interval eye drifts to improve visual discrimination. The last day/first day ratios of these off-fixation percentages in the second interval were 0.954 (<0.5°) and 0.995 (<1°), suggesting no reduction of eye drifts after training. Therefore, perceptual learning in these two-interval tasks (Figures 1 and 2) was little affected by eye movement either.

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