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Task relevancy and demand modulate double-training enabled transfer of perceptual learning

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ABSTRACT

Location-specific perceptual learning can be rendered transferrable to a new location with double training, in which feature training (e.g., contrast) is accompanied by additional location training at the new location even with an irrelevant task (e.g. orientation). Here we investigated the impact of relevancy (to feature training) and demand of location training tasks on double training enabled learning transfer. We found that location training with an irrelevant task (Gabor vs. letter judgment, or contrast discrimination) limited transfer of Vernier learning to the trained orientation only. However, performing a relevant suprathreshold orthogonal Vernier task prompted additional transfer to an untrained orthogonal orientation. In addition, the amount of learning transfer may depend on the demand of location training as well as the double training procedure. These results characterize how double training potentiates the functional connections between a learned high-level decision unit and visual inputs from an untrained location to enable transfer of learning across retinal locations.

1. Introduction

Visual perceptual learning improves discrimination of many basic visual features, such as contrast, orientation, Vernier, and texture. A key feature of it is that learning is often specific to the trained retinal location and orientation (Ahissar & Hochstein, 1997; Crist et al., 1997; Fahle, 1994, 1997; Karni & Sagi, 1991; Saarinen & Levi, 1995; Schoups, Vogels, & Orban, 1995; Shiu & Pashler, 1992; Yu, Klein, & Levi, 2004). The location and orientation specificities place important constraints on various perceptual learning models and theories (Adini, Sagi, & Tsodyks, 2002; Bejjanki et al., 2011; Dosher & Lu, 1998; Law & Gold, 2009; Mollon & Danilova, 1996; Poggio, Fahle, & Edelman, 1992; Teich & Qian, 2003; Zhaoping, Herzog, & Dayan, 2003), as it is suggested that modeling the neural mechanisms underlying perceptual learning must account for these specificities (Tsodyks & Gilbert, 2004).

However, in recent studies we demonstrated that location specificity and orientation specificity can be decoupled from perceptual learning in a variety of visual tasks with appropriate training procedures (Xiao et al., 2008; Zhang, Xiao, et al., 2010; Zhang, Zhang, et al., 2010). For example, with a feature-plus-location double training procedure, perceptual learning of contrast discrimination (feature training), which is otherwise location specific, can transfer completely to a new location following additional location training at the new location using an irrelevant orientation discrimination task (Xiao et al., 2008). Similarly, with a training-plus-exposure (TPE) procedure, perceptual learning of orientation in foveal vision, which is otherwise specific to the trained orientation, can transfer completely to an orthogonal orientation if an observer is also passively exposed to the orthogonal orientation while performing an irrelevant contrast discrimination task (Zhang, Zhang, et al., 2010).

These transfer results suggest that at least in some cases perceptual learning is more a general learning process and most likely occurs at a high decision level of information processing beyond the retinotopic and orientation selective visual cortex (Xiao et al., 2008; Zhang, Zhang, et al., 2010; Zhang, Xiao, et al., 2010). This argument is supported by a recent fMRI study indicating that the site of perceptual learning may be located in the human medial front cortex, which is also the site of perceptual decision making (Kahnt et al., 2011). We thus proposed a rule-based learning theory to explain visual perceptual learning and its specificity and transfer (Zhang, Zhang, et al., 2010). This theory posits that a high-level decision unit learns the rules for performing a visual task through training. However, the learned rules cannot be applied to a new location or orientation automatically because the decision unit cannot functionally connect to the visual inputs representing the new location or orientation with sufficient strength. These inputs are unattended or even suppressed during training when attention is allocated to the trained location or orientation (Gal et al., 2009; Sylvester et al., 2009). It is double training and TPE training that

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reactivate these new inputs, so that the functional connections can be strengthened to enable rule application and transfer of learning.

The current study manipulated the task relevancy (to feature training) and the demand of location training and investigates their impact on the transfer of feature (Vernier) learning from a diagonal quadrant of the visual field. We used three levels of task relevance (passive stimulus exposure, irrelevant, and relevant) and three demand levels (passive stimulus exposure, suprathreshold, and near-threshold) with the location training. Here passive stimulus exposure was least task relevant and least demanding, and was therefore used in both categories as baselines. Vernier learning is found to be strictly specific to the trained location (Xiao et al., 2008), so its transfer to a new location would serve as an excellent indicator of the impact of location training under various task relevancy and demand conditions. Our results show that an observer's active participation in a visual task at the new location, even a very simple one, rather than passive exposure to the stimuli is necessary for Vernier learning to transfer. Moreover, task-irrelevant location training limits learning transfer to only the trained Vernier orientation, but a relevant suprathreshold orthogonal Vernier task allows additional learning transfer to the orthogonal orientation. In addition, the amount of learning transfer may depend on the demand level in the location training task as well as the particular double training procedure (simultaneous or sequential). In the context of our rule-based perceptual learning theory, these results characterize double training potentiating the functional connections between a learned high-level decision unit and new visual inputs from an untrained retinal location, which makes the transfer of perceptual learning possible.

2. Methods

2.1. Ob a a a

Forty observers (undergraduate students in their early twenties at Beijing Normal University) with normal or corrected-to-normal vision participated in this study. All were new to psychophysical experiments and were unaware of the purpose of the study. Informed consent was obtained from each observer before data collection.

The stimuli were generated by a Matlab-based WinVis program (Neurometrics Institute, Oakland, CA) and presented on a 21-in. Sony G520 color monitor (2048 pixel × 1536 pixel, 0.19 mm × 0.19 mm per pixel, 75 Hz frame rate). The mean luminance was 50 cd/m^2. 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, and a chin-and-head rest helped stabilize the head of the observer. The viewing distance was 1.5 m. Experiments were run in a dimly lit room.

2.2. S

The Vernier stimulus consisted of a pair of identical Gabor patches (Gaussian windowed sinusoidal gratings) on a mean luminance screen background, which was centered in a visual quadrant at 5° retinal eccentricity (Fig. 1A). The two Gabors had the same spatial frequency (3 cpd), fixed phase (90°), 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 with the Vernier offset jittered at ±15 arcmin. The contrasts of the two Gabors were set at 0.47 and 0.47 + ΔC.

2.3. P c

Vernier and contrast discrimination thresholds were measured with a single-interval discrimination 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 fixation cross 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 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.

2.4. S a c

The amount of perceptual learning was quantified as the Percent Improvement (PI), where $PI = (Thresh_{Pre} - Thresh_{Post})/Thresh_{Pre}$. We hypothesized that thresholds were lower after training in perceptual learning experiments, so that one-tailed hypothesis tests were used.

3. Results

3.1. Ba : a a a a a ca

We first studied whether passive exposure to stimuli at the transfer location would enable the transfer of Vernier learning. Passive stimulus exposure was least task-relevant and required the least effort by the observer, so this measure provided baselines for the impacts of task relevancy and demand of location training on learning transfer. Sixteen observers practiced Vernier discrimination at a horizontal or vertical orientation in one of four visual quadrants (ori1_loc1) at 5° retinal eccentricity while an orthogonal Vernier in the diagonal quadrant (ori2_loc2) was flashed simultaneously for the same 200 ms duration (Fig. 1A). The offset of the flashed Vernier was randomly set at ±15 arcmin, or approximately ±2.5 times the mean pre-training Vernier threshold. Because nearly all attention was allocated to Vernier discrimination at the trained location, the flashed Vernier was only passively viewed by an observer. Significant learning was evident at the trained orientation and location (ori1_loc1, Mean Percent Improvement (MPI) = 27.3 ± 2.9%, < 0.001, paired -test) after six to seven 2-h daily sessions (Fig. 1B and C). However, learning transferred little to the same or orthogonal orientations in the diagonal visual quadrant with passive stimulus exposure (ori1_loc2, MPI = −0.5 ± 4.4%, = 0.55; ori2_loc2, MPI = 1.2 ± 4.0%, = 0.39), as well as the orthogonal orientation at the trained location (ori2_loc1, MPI = 1.5 ± 5.8%, = 0.40) (Fig. 1B and C). These results indicate that mere passive exposure to the stimuli at the transfer location cannot replace active location training to override the specificity of Vernier learning revealed in our previous study with identical stimuli (Xiao et al., 2008).

3.2. D b a : a a ca a a a a a

Among the 16 observers in the passive stimulus exposure experiment (Fig. 1), one did not learn (Vernier performance

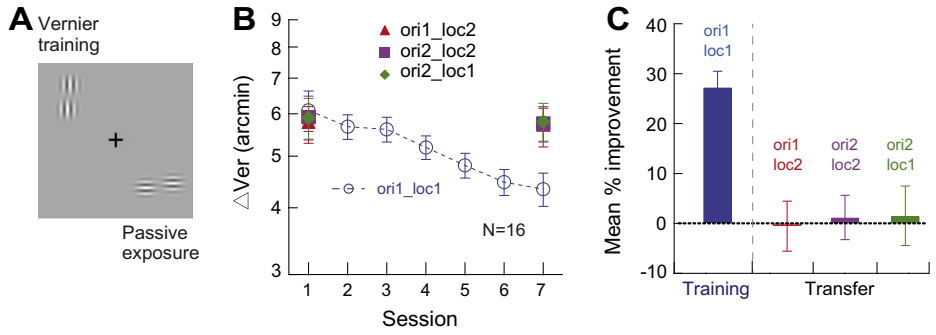


Fig. 1. Transfer of Vernier learning to a diagonal quadrant where an orthogonal Vernier was passively exposed. (A) Stimuli. Observers practiced Vernier discrimination at ori1_loc1 while passively exposed to an orthogonal Vernier flashed simultaneously in the diagonal quadrant (ori2_loc2). (B) The mean session-by-session threshold changes in the trained condition and pre- and post-training thresholds at the transfer conditions. (C) The MP|s of Vernier performance in the trained condition (left bar) and untrained transfer conditions (right three bars).

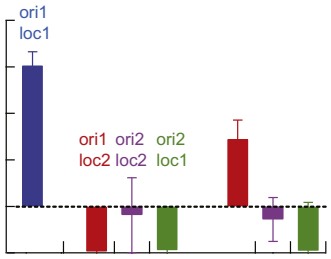
improved by <3%) and two showed significant transfer (the transfer index (T|), defined as the ratio of transfer/training performance improvements, was >0.5). The remaining thirteen showed little or no improvement in performance in the transfer conditions (mean T| = −0.15 ± 0.14). We were able to call eleven of these thirteen observers back and split them into two groups, each performing a suprathreshold task either irrelevant or relevant to feature learning. The first group of five observers in the current experiment judged whether a pair of Gabors (Fig. 2A, same as the flashing Gabors in Fig. 1A, presented on 80% of the trials,) or an uppercase letter E (20% of the trials) appeared in the diagonal transfer quadrant for four sessions. Here the observers were forced to perform an irrelevant, non-demanding suprathreshold task (mean accuracy = 99.7%) at the transfer location. For these five observers, the previous Vernier training produced significant improvement at ori1_loc1 (MP| = 30.3 ± 2.9%, < 0.001, Fig. 2B and C), but learning did not transfer to untrained ori1_loc2 (MP| = −9.7 ± 8.0%, = 0.85), ori2_loc2 (MP| = −1.9 ± 8.1%, = 0.59), and ori2_loc1 at the trained location (MP| = −9.5 ± 9.4%, = 0.81) (Fig. 2B and C). After the new Gabors vs. E judgments, Vernier performance was improved at ori1_loc2 (MP| = 14.5 ± 4.0%, = 0.012), but not at orthogonal ori2_loc2 (MP| = −2.8 ± 4.7%, = 0.71) and ori2_loc1 (MP| = −9.6 ± 10.4%, = 0.79) (Fig. 2B and C), indicating that location training with an irrelevant suprathreshold task can enable the transfer of Vernier learning across retinal locations, but the transfer is limited to the trained orientation. On the other hand, the lower MP| at ori1_loc2 (14.5% vs. 30.3%) appeared to indicate partial transfer of learning (= 0.047 for MP|s at ori1_loc1 vs. ori1_loc2). However, it was unclear whether the partial transfer truly resulted from location training with an irrelevant suprathreshold task, or from a performance ceiling effect at the transfer location (the post-training thresholds were 4.34 ± 0.47 arcmin at ori1_loc1 and 4.50 ± 0.16 arcmin at ori1_loc2, = 0.37) combined with the lower pre-training thresholds at ori1_loc2 (Fig. 2B). In the latter case the transfer of learning could actually be complete.

In our previous study (Xiao et al., 2008) double training enabled complete transfer of learning regardless of whether feature and location training (with an irrelevant but demanding near-threshold task) was performed simultaneously or sequentially. However, the above results would suggest that demanding location training might be unnecessary if the transfer of learning is indeed complete. Would the above findings of orientation specificity in learning transfer and potentially complete learning transfer be replicable in a simultaneous double training procedure? We had eight new observers practice Vernier discrimination at ori1_loc1 and judge the same Gabors or E in the diagonal quadrant in alternating blocks of trials in a same session for five sessions. Training improved Vernier performance at ori1_loc1 by 29.6 ± 4.0% (< 0.001), nearly identical to the 30.3 ± 2.9% MP| in Fig. 2B. Vernier learning again transferred to the same trained orientation ori1_loc2 only (MP| = 18.2 ± 6.6%, = 0.015), but not to orthogonal ori2_loc2 (MP| = 5.1 ± 4.9%, = 0.17) and ori2_loc1 (MP| = 4.3 ± 5.1%, = 0.21) (Fig. 2D and E). These results confirmed that the transfer of learning was specific to the trained orientation under the current double training conditions. However, the transfer was clearly partial with lower MP| at ori1_loc2 than at ori1_loc2 (= 0.014) and similar pre-training thresholds.

3.3. D b a : a a ca a a a a a a d a

The second group of six observers who did not show much transfer after passive stimulus exposure (Fig. 1) judged an orthogonal Vernier with the offset set at five times the threshold after passive stimulus exposure at the transfer location for four sessions (Fig. 3A). Since the offset was well above threshold, the task was not demanding (mean accuracy = 99.1%), but this time the task was relevant to feature (Vernier) learning. For these six observers, previous Vernier training produced significant improvement at ori1_loc1 (MP| = 24.1 ± 3.8%, < 0.001), and learning did not transfer to ori1_loc2 (MP| = 0.3 ± 3.1%, = 0.47), ori2_loc2 (MP| = 2.4 ± 2.3%, = 0.18), and ori2_loc1 (MP| = −5.6 ± 8.7%, = 0.73) (Fig. 3B and C). However, after the suprathreshold Vernier judgments at ori2_loc2, Vernier learning transferred not only to ori1_loc2 (MP| = 15.5 ± 3.1%, = 0.002), but also to the orthogonal ori2_loc2 (MP| = 20.4 ± 4.6%, = 0.003) and ori2_loc1 (MP| = 13.2 ± 5.2%, = 0.026) (Fig. 3B and C). Moreover, after this two-phase double training there was no significant difference in performance improvement among the trained condition (MP| = 18.6 ± 5.0%, = 0.007) and three transfer conditions (= 0.30, repeated measures ANOVA).

We again had seven new observers repeat the experiment in a simultaneous procedure. They practiced Vernier discrimination at ori1_loc1 and judged suprathreshold orthogonal Vernier (five times the mean pre-training threshold) at ori2_loc2 in alternating blocks of trials in the same session for five sessions. Consistent with the sequential double training data, Vernier learning at ori1_loc1 (MP| = 38.9 ± 4.3%, < 0.001, which is higher than the magnitude in the sequential condition described above), transferred to not only ori1_loc2 (MP| = 17.8 ± 5.8%, = 0.011), but also orthogonal ori2_loc2 (MP| = 20.9 ± 4.9%, = 0.003) and ori2_loc1 (MP| = 18.7 ± 8.4%, = 0.034) (Fig. 3D and E). However, as in Fig. 2D, the simultaneous procedure only produced partial transfer (= 0.015 for the contrast between the training MP| and three transfer MP|s, repeated measures ANOVA). Taking Figs. 2 and 3 results together, there appears to be a trend that location training with a



Gabors/E?

suprathreshold task may enable complete transfer in a sequential double-training procedure, but only partial transfer in a simultaneous procedure.

In addition, we ran a control experiment in which five new observers performed only the same suprathreshold Vernier task (five times the mean pre-training threshold) at ori2_loc2 for four

sessions. This suprathreshold task had no impact on the Vernier thresholds at ori1_loc2, ori2_loc2, and ori2_loc1 (Fig. 3F), excluding the possibility that the transfers described above were caused by the suprathreshold Vernier task alone.

3.4. D b a : a a ca a a a b a a -

We know from our previous study that learning can transfer completely to a new location if feature training is accompanied with irrelevant but demanding near-threshold training at the new location (Xiao et al., 2008). Here we examined whether this complete transfer was still specific to the trained orientation. Nine

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