



Co-learning analysis of two perceptual learning tasks with identical input stimuli supports the reweighting hypothesis

Chang-Bing Huang^{a,b}, Zhong-Lin Lu^{a,c,*}, Barbara A. Doshier^d

^a Laboratory of Brain Processes (LOBES), Departments of Psychology, University of Southern California, Los Angeles, CA 90089, USA

^b Key Laboratory of Behavioral Science, Institute of Psychology, Chinese Academy of Sciences, 4A Datun Road, Chaoyang District, Beijing 100101, China

^c Department of Psychology, The Ohio State University, 1835 Neil Avenue, Columbus, OH 43210, USA

^d Department of Cognitive Sciences, University of California, Irvine, CA 92697, USA

ARTICLE INFO

Article history:

Received 1 June 2011

Received in revised form 2 November 2011

Available online 12 November 2011

Keywords:

Perceptual learning

Vernier

Bisection

Representation enhancement

Selective reweighting

ABSTRACT

Perceptual learning, even when it exhibits significant specificity to basic stimulus features such as retinal location or spatial frequency, may cause discrimination performance to improve either through enhancement of early sensory representations or through selective re-weighting of connections from the sensory representations to specific responses, or both. For most experiments in the literature, the two forms of plasticity make similar predictions (Doshier & Lu, 2009; Petrov, Doshier, & Lu, 2005). The strongest test of the two hypotheses must use training and transfer tasks that rely on the same sensory representation with different task-dependent decision structures. If training changes sensory representations, transfer (or interference) must occur since the (changed) sensory representations are common. If instead training re-weights a separate set of task connections to decision, then performance in the two tasks may still be independent. Here, we performed a co-learning analysis of two perceptual learning tasks based on identical input stimuli, following a very interesting study of Fahle and Morgan (1996) who used nearly identical input stimuli (a three dot pattern) in training bisection and vernier tasks. Two important modifications were made: (1) identical input stimuli were used in the two tasks, and (2) subjects practiced both tasks in multiple alternating blocks (800 trials/block). Two groups of subjects with counter-balanced order of training participated in the experiments. We found significant and independent learning of the two tasks. The pattern of results is consistent with the reweighting hypothesis of perceptual learning.

© 2011 Elsevier Ltd. All rights reserved.

1. Introduction

Practice makes better performance, even for very simple visual tasks. This perceptual learning effect could be very specific to the trained tasks, eye of origin, orientation, motion direction, and retinal location, a property that has usually served as an important basis for claims of plasticity in primary visual cortex (Ahissar & Hochstein, 1993, 1997; Crist et al., 1997; Fahle & Morgan, 1996; Fiorentini & Berardi, 1997; Liu & Weinshall, 2000; Poggio, Fahle, & Edelman, 1992; see also Fine and Jacobs (2002) and Gilbert, Sigman, and Crist (2001) for reviews). On the other hand, a number of researchers (Doshier & Lu, 1998, 1999; Law & Gold, 2008; Lu, Hua et al., 2010; Mollon & Danilova, 1996) have proposed that the observed specificity of perceptual learning could have resulted from learning to “read-out” the most informative outputs from the unchanged sensory representations (the “selective re-weighting

hypothesis”). Following Petrov, Doshier, and Lu (2005) and Doshier and Lu (2009), we refer to the first view as the “sensory representation enhancement” hypothesis, which claims plasticity with alterations in the earliest possible visual areas (Petrov, Doshier, & Lu, 2005).

Attempts to infer the locus/loci of perceptual learning have generated mixed results. Most physiological research in animals failed to find behavior-related changes in visual area V1, a site favored by the sensory representation enhancement hypothesis (Crist, Li, & Gilbert, 2001; Ghose, Yang, & Maunsell, 2002; Rainer, Lee, & Logothetis, 2004; Yang & Maunsell, 2004; but see Hua et al. (2010)). On the contrary, most fMRI and PET studies found significant activation changes in early visual areas following perceptual learning, although the signs of the changes were not consistent: increases in the BOLD fMRI responses (Bao et al., 2010; Furmanski, Schluppeck, & Engel, 2004; Schwartz, Maquet, & Frith, 2002; Yotsumoto, Watanabe, & Sasaki, 2008) but decreases in PET signals (Schiltz et al., 1999) have been reported.

Psychophysically, the locus of learning has often been inferred from a “Train-Then-Test (T3)” paradigm in which subjects were

* Corresponding author at: Laboratory of Brain Processes (LOBES), Department of Psychology, Ohio State University, Columbus, OH 43210, USA.

E-mail address: lu.535@osu.edu (Z.-L. Lu).

usually trained to perform a certain task in one stimulus condition and location, e.g., an orientation identification task at 45° in the lower-left visual field, and tested in other conditions and/or locations after training, e.g. -45° in the lower-left visual field or 45° in the upper-right visual field. Based on this “T3” paradigm, many studies have found that learning effects were at least partially specific to the trained feature and/or location. This specificity has generally been interpreted as favoring the sensory representation enhancement hypothesis. However, a systematic task analysis is necessary to interpret various specificity results and design more diagnostic tests for the level of perceptual learning (Petrov, Doshier, & Lu, 2005).

The three most commonly used training and transfer tests in the T3 paradigm involve either (1) distinct sensory representations followed by different task response structures (e.g., orientation identification around 45° in the lower-left visual field followed by motion direction identification around 45° in the lower-right visual field), or (2) or the same task followed by independent copies of the task-response structure (e.g., orientation identification around 45° in the lower-left visual field followed by orientation identification around -45° in the lower-right visual field), or (3) the same task-response structure but independent sets of connections (e.g., orientation identification around 45° in the lower-left visual field followed by orientation identification around 45° in the upper-right visual field). The results from these types of learning and transfer tests cannot distinguish the sensory representation enhancement (low-level) and selective reweighting hypotheses, because changes of either sensory representation or weights that connect it to decision would result in learning that is specific to the sensory representation.

A strong test of the two hypotheses requires the application of training and test stimuli that rely on the same sensory representation but with different task-dependent decision structures (Petrov, Doshier, & Lu, 2005). If training changes sensory representations, transfer (or interference) must occur since the (changed) sensory representational coding is common. If instead, training re-weights a separate set of task connections to decision, performance in the two tasks would still be independent.

In this paper, we performed a co-learning analysis of two perceptual learning tasks with identical input stimuli, following a very interesting study of Fahle and Morgan (1996) who used nearly identical input stimuli (a three dot pattern) in training bisection and vernier tasks (Fahle & Morgan, 1996). Two important modifications were made: (1) Identical input stimuli were used in the two tasks, and (2) subjects practiced in both tasks in multiple alternating blocks. The second modification is essential for distinguishing independent and competitive (push-pull) co-learning (Petrov, Doshier, & Lu, 2005, 2006). Our results are consistent with the selective reweighting hypothesis.

2. Methods

2.1. Subjects

Twelve adults (21–31 yrs) with normal or corrected-to-normal vision participated in the study. Among them, four (including author CBH) were trained in a replication of Fahle and Morgan (1996), and the other eight were trained with a modified design in which *identical* stimuli were used for the bisection and vernier tasks. Written informed consent was obtained from all the subjects.

2.2. Stimuli and apparatus

Stimuli used in the replication part were similar to those of Fahle and Morgan (1996; Fig. 1A and B). The upper and lower dots, with an equal diameter of $70''$ and separated by $700''$ from center to

center, never changed their positions. The center dot was closer to the upper or lower dot in the bisection task, but placed to the left or right of the imaginary vertical line through the centers of the upper and lower dots in the vernier task.

For the new experiment, we developed a novel layout in which the vernier and bisection tasks shared the same input stimuli (Fig. 1C). The upper and lower dots were separated and positioned just as those in the replication study. The center dot was, however, positioned at one of four possible locations ((Vt,Bt), (-Vt,Bt), (-Vt,-Bt) and (Vt,-Bt)) in a given trial, based on the pre-determined vernier (Vt) and bisection (Bt) threshold offsets. Subjects were asked to respond based on the specific task instruction.

All stimuli were generated by a notebook PC running Matlab programs based on PsychToolBox 2.54 (Brainard, 1997; Pelli, 1997), and projected through a ViewSonic PJ 250 onto a rear-project screen. The display had a resolution of 1024×768 and subtended $24' \times 18'$ at the viewing distance of 7.45 m. Each pixel subtended $1.4'' \times 1.4''$. The background luminance was 25 cd/m^2 ; the dots' luminance was 105 cd/m^2 . Subjects viewed the display binocularly.

2.3. Design and procedure

The same design was used in the replication and the new experiments. Thresholds at 70.7% correct for both vernier and bisection tasks were first measured for each subject with a 2-down 1-up staircase in 80 trials. The measured threshold offsets were used and kept fixed throughout the rest of the experiment.

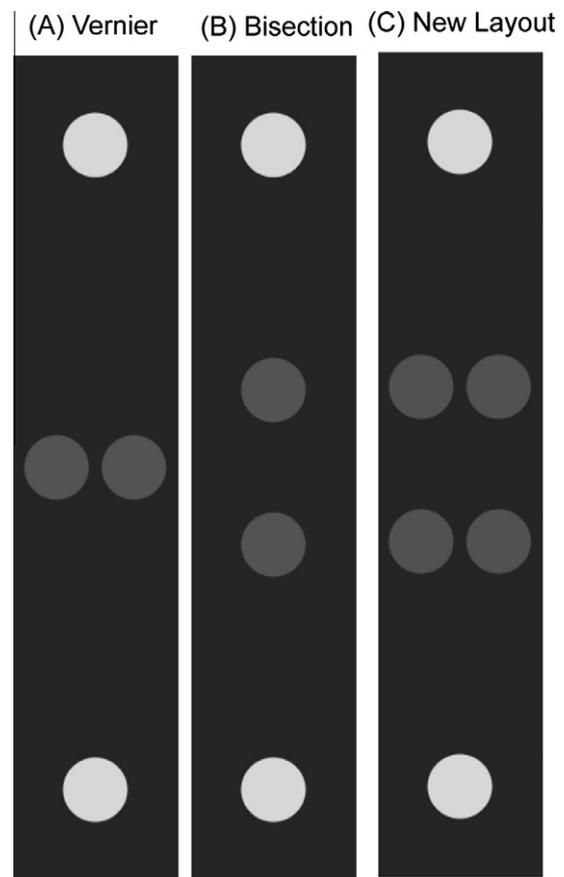


Fig. 1. Stimuli layout. (A and B) Stimuli used to replicate Fahle and Morgan's (1996). For either the vernier or bisection task, the center dot can be in two possible locations. In the new design (C), the center dot can be positioned at one of four locations defined by pre-determined vernier and bisection thresholds. In the figure, we lowered the luminance of the center dot to demonstrate its possible locations. It had the same luminance as the upper and lower dots in the experiments.

The learning dynamics were tested by alternately training the two tasks for several cycles of repetition. The alternation design is necessary to distinguish independent co-learning from learning in which the two tasks interact in training. The specific training occurred within a “ $mA-nB$ ” design, in which “ m ” and “ n ” are the numbers of blocks, and “ A ” and “ B ” denote the two different tasks. There were a total of 60 blocks, distributed across seven sessions. The presentation sequence was either “ $8A-2A8B-2B8A-2A8B-2B8A-2A8B-2B$ ” or “ $8B-2B8A-2A8B-2B8A-2A8B-2B8A-2A$ ”, depending on the task that was first trained. Half of the subjects were first trained with the vernier task and the other half with the bisection first. There were 80 trials in each block. Within each block, the task was fixed. Each task was trained in three cycles of 10 blocks each. All task switches occurred in midsession, avoiding potential confounds of overnight consolidation or forgetting (Karni et al., 1994). Subjects were informed of the transition between task blocks.

The stimulus presentation time was 150 ms. An inter-trial interval of 1 s was provided. Subjects were required to report with the left and right arrow keys when performing the vernier task, and up and down arrow keys in the bisection task. To reduce fatigue (Censor & Sagi, 2009b), we asked subjects to take a 2-min mandatory break between blocks. Subjects could also elect to take short breaks at will.

2.4. Augmented Hebbian reweighting model (AHRM)

To implement the reweighting hypothesis in modeling the learning dynamics and switch costs of perceptual learning in non-stationary contexts, Petrov, Doshier, and Lu proposed an augmented Hebbian reweighting model (AHRM) of perceptual learning (Petrov, Doshier, & Lu, 2005, 2006). Briefly, the AHRM consisted of sensory representation units that encode input images as activation patterns, a task-specific decision unit that receives weighted inputs from the sensory representation units, an adaptive bias unit that accumulates a running average of the response frequencies and works to balance the frequency of the two responses, and a feedback unit that makes use of external feedback when it is presented. Learning in the model occurs exclusively through incremental Hebbian modification of the weights between the sensory representation units and the decision unit, while the early sensory representations remain unchanged throughout training. Detailed descriptions of the augmented Hebbian reweighting model can be found in Petrov, Doshier, and Lu (2005, 2006). We have modified the AHRM to model the results of the present experiment.

2.4.1. Sensory representation units

The sensory representation subsystem, or “receptive field”, approximates the point-spread function of the visual system with 20 arrayed Gaussian blobs with spatial extent $\sigma = 30''$. The setup is similar to Poggio et al. (1992) and the same for both the vernier and bisection tasks. Performance of the model is robust to the positioning of these blobs. This implements an alternative sensory representation system from the “orientation \times spatial frequency” representation used by Petrov, Doshier, and Lu (2005, 2006). The position representation is more suited to the two tasks studied here.¹

The input image I was first filtered by the 20 units (dot-product). The activation maps were pooled across space and normalized to the total energy in the 20 units, which was then constrained by

¹ Another approach is to build the sensory representation of our stimuli using a network of neurons that are tuned to orientations and spatial frequencies (such as V1 cells) in each spatial location. After pooling over the outputs of the neurons in each location, the output of the network would be very similar to those of the array of Gaussian blobs.

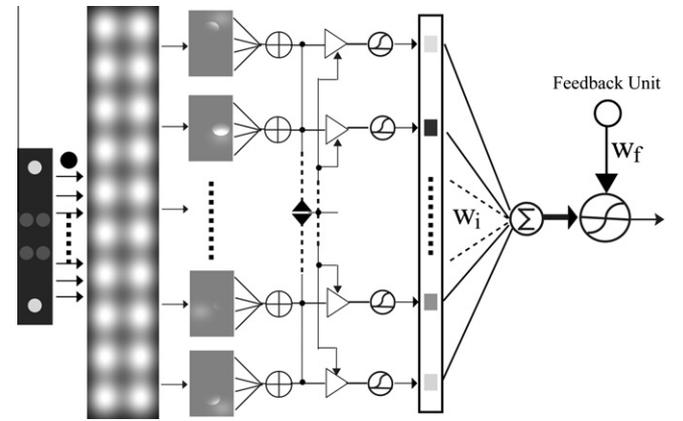


Fig. 2. The augmented Hebbian reweighting model (AHRM) (Petrov, Doshier, & Lu, 2005, 2006) with a different sensory representations system for the two tasks in this study.

an activation function to limit their dynamic range. Representational noise ε_1 with mean 0 and standard deviation σ_1 was then added to the outputs of the units to model various inefficiencies in the visual system (Lu & Doshier, 1999, 2008). The activation of sensory representation units was rectified to be non-negative, range-limited and saturated at high inputs with gain parameter γ_1 .

$$E_i(x, y) = RF_i(x, y) \cdot I, \quad (1)$$

$$A'(i) = \sum_{x, y} E_i(x, y), \quad (2)$$

$$A'(i) = \frac{A'(i)}{k + \sum A'(i)} + \varepsilon_1, \quad (3)$$

$$A(i) = \begin{cases} \frac{1 - e^{-\gamma_1 A'(i)}}{1 + e^{-\gamma_1 A'(i)}} A_{\max}, & \text{if } A'(i) \geq 0, \\ 0, & \text{otherwise,} \end{cases} \quad (4)$$

where $i = 1, \dots, 20$ in all these equations.

2.4.2. Task-specific decision units

The decision subsystem assembles the sensory information using the current weights w_i and the current top-down bias b :

$$u = \sum_{i=1}^{20} w_i A_i - w_b b + \varepsilon_2, \quad (5)$$

where w_i denotes the current weights of each Gaussian blob. Two independent sets of weights are used for the vernier and bisection tasks. Generally w_i is negative for detectors in the first column and positive in the second column for the vernier task, and positive for detectors in the first five rows and negative in the last five rows for bisection task (Fig. 2). Gaussian noise ε_2 with mean 0 and standard deviation σ_d models random fluctuations in the decision-making process (σ_{d1} for the vernier task and σ_{d2} for the bisection task). In the current experimental settings, response bias toward one or the other response (e.g., left vs right in vernier offset judgment) is minimal and thus we omitted the bias term in the following analysis ($w_b = 0$), although it may be very important for learning in some non-stationary contexts (Liu, Lu, & Doshier, 2010; Petrov, Doshier, & Lu, 2005, 2006). The early activation o' of the unit is computed with a sigmoidal function from the early input u with gain γ_2 :

$$G(u) = \frac{1 - e^{-\gamma_2 u}}{1 + e^{-\gamma_2 u}} A_{\max}, \quad (6)$$

$$o' = G(u) \quad (\text{early}). \quad (7)$$

The model generates a “left” response in the vernier task or “up” response in the bisection task if o' is negative, and a “right” response in the vernier task or “down” response in the bisection task if o' is positive.

2.4.3. Augmented Hebbian learning algorithm

In the AHRM, feedback, if present, is encoded by the feedback unit and sent as a top-down input to the decision unit. This new input-weighted F adds to the early input u driving the decision unit, which changes its activation to a new, late activation level o according to the following equation:

$$o = G(u + w_f F) \quad (\text{late}). \quad (8)$$

All learning happens during this late phase (O'Reilly & Munakata, 2000). The impact of feedback depends upon the weight w_f on the feedback input. The late activation is driven to $\pm A_{\max} = \pm 0.5$ when feedback $F = \pm 1$ is present and the feedback weight is relatively high. Lower feedback weights may simply shift the activation slightly.

In the AHRM, the only mechanism for long-term changes due to learning operates on the synaptic strengths w_i of the connections between the sensory units RF_i and the decision unit. The Hebbian rule is exactly the same with and without feedback. Each weight change depends on the activation A_i of the pre-synaptic sensory unit and the activation o of the postsynaptic decision unit relative to the baseline.

$$\delta_i = \eta A_i (o - \bar{o}), \quad (9)$$

$$\Delta w_i = (w_i - w_{\min})[\delta_i]_- + (w_{\max} - w_i)[\delta_i]_+, \quad (10)$$

$$[\delta_i]_- = \begin{cases} \delta_i, & \text{if } \delta_i < 0; \\ 0, & \text{otherwise;} \end{cases} \quad [\delta_i]_+ = \begin{cases} \delta_i, & \text{if } \delta_i > 0; \\ 0, & \text{otherwise.} \end{cases} \quad (11)$$

$$\bar{o}(t+1) = \rho o(t) + (1 - \rho)\bar{o}(t). \quad (12)$$

Eq. (10) constrains the weights within bounds ($[W_{\min}, W_{\max}]$) by scaling δ_i in proportion to the remaining range (O'Reilly & Munakata, 2000). The operation $[\delta_i]_-$ returns δ_i if $\delta_i < 0$ and 0 otherwise; $[\delta_i]_+$ returns δ_i if $\delta_i > 0$ and 0 otherwise. Continuous reinforcement ($\delta_i > 0$) drives the corresponding weight exponentially toward the upper bound (w_{\max}); repeated inhibition ($\delta_i < 0$) drives the corresponding weight exponentially toward the lower bound (w_{\min}). Eq. (11) subtracts the long-term average \bar{o} of postsynaptic activation from its current value o , causing the Hebbian term δ_i to track systematic stimulus-response correlations rather than mere response bias.

2.5. Model fit and statistical analysis

For the data from the new paradigm, the Analysis of Variance (ANOVA) was first performed to test if training sequence affected learning outcomes significantly, i.e. to determine whether there was a significant difference in learning a specific task (vernier or bisection) between the four subjects who were first trained with the vernier task and the four who were first trained with the bisection task. In doing so, training blocks and sequences were treated as two independent factors and all data were normalized to initial performance for all subjects. The ANOVA revealed no significant effect of training sequence on learning either task (see Section 3.2). We pooled the eight subjects' data in subsequent analysis.

The average learning curves of the vernier and bisection tasks were statistically compared based on a regression analysis:

$$PC_{ver} = \alpha_v \log(T) + \beta_v, \quad (13)$$

$$PC_{bis} = \alpha_b \log(T) + \beta_b, \quad (14)$$

where PC stands for percent correct in performing the vernier and bisection tasks and T is the number of training block. Four sets of regression analysis were performed: (1) the learning curves are different for the two tasks, i.e. $\alpha_v \neq \alpha_b$ and $\beta_v \neq \beta_b$; (2) the two curves have the same slope, i.e. $\alpha_v = \alpha_b$ and $\beta_v \neq \beta_b$; (3) the two curves have the same Y-axis intercept, i.e. $\alpha_v \neq \alpha_b$ and $\beta_v = \beta_b$; (4) the two curves are identical, i.e. $\alpha_v = \alpha_b$ and $\beta_v = \beta_b$. The goodness-of-fit was gauged by the r^2 statistic and compared with an F -test for nested models:

$$r^2 = 1.0 - \frac{\sum (PC_i^{pred} - PC_i^{meas})^2}{\sum [PC_i^{meas} - \text{mean}(PC_i^{meas})]^2}, \quad (15)$$

$$F(df_1, df_2) = \frac{(r_{full}^2 - r_{red}^2)/df_1}{(1 - r_{full}^2)/df_2}, \quad (16)$$

where PC_i^{meas} and PC_i^{pred} denote measured values of percent correct and the corresponding model predictions, k_{full} and k_{red} are the number of parameters for any two nested models, $df_1 = k_{full} - k_{red}$ and $df_2 = N - k_{full}$ are degrees of freedom for the test, and N is the total number of data points. When comparing the learning curves, we also calculated the standard deviations of the learning rates using a bootstrap method.

The AHRM was implemented in a MATLAB program. The program takes grayscale images as inputs, produces binary (left/right for the vernier task or up/down for the bisection task) responses as outputs, and learns on a trial-by-trial basis. The model parameters are listed in Table 1. Five parameters, including representation noise (σ_1), decision noise of the vernier task (σ_{d1}) and the bisection task (σ_{d2}), learning rate (η ; same for both the vernier and bisection tasks), and activation function non-linearity ($\gamma_1 = \gamma_2 = \gamma$), were adjusted to fit the average experimental data. The spatial extent (σ) of the Gaussian blob was set at 30, slightly less than the radius of the dots in the stimuli. Our simulation revealed that the spatial extent of the blob over a wide range did not affect the results. The initial “read-out” weights were set at ± 0.16 . We first derived the initial guesses of the five parameters from a coarse grid search. Using a non-linear least-square algorithm, we then minimized $\sum (PC_i^{pred} - PC_i^{meas})^2$ based on the initial guesses. The goodness-of-fit was evaluated by the r^2 statistic (as Eq. (14)). The model, just as human subjects, went through 60 blocks of trials with 30 blocks for each task and 80 trials in each block. A bootstrap procedure was used to generate confidence intervals. In each bootstrap step, we sampled performance curves from eight simulations, corresponding to eight subjects, to calculate the average learning curve of eight simulated observers. This was repeated 1000 times. Following standard practice in bootstrap, we computed the mean and standard deviations from the 1000 learning curves.

Table 1
AHRM parameters.

Parameter	Value
<i>Parameters set a priori</i>	
Maximum activation level	$A_{\max} = \pm 0.5$
Weight bounds	$w_{\max}/w_{\min} = \pm 1$
Running average rate	$\rho = 0.0125$
Normalization constant	$k = 0$
Size of the Gaussian detector	$\sigma = 30''$
Initial weight	$w_{ini} = 0.16$
Feedback weight	$w_f = 1.0$
<i>Parameters optimized to fit the average data</i>	
Representation noise	$\sigma_1 = 0.0223$
Decision noise for vernier task	$\sigma_{d1} = 0.00011$
Decision noise for bisection task	$\sigma_{d2} = 0.011$
Learning rate	$\eta = 0.0926$
Activation function non-linearity	$\gamma_1 = \gamma_2 = 2.38$

3. Results

3.1. Replication of Fahle and Morgan (1996)

Four subjects were trained to replicate Fahle and Morgan (1996). Fig. 3 plots the average percent correct as a function of training blocks. All subjects' performance improved even though the magnitude varied across subjects and sessions, consistent with Fahle and Morgan (1996). It is obvious that most of the learning happened during the first two training sessions (the first 20 blocks, 10 blocks or 800 trials for each task), with an average performance increase from 74% to 87% for the vernier task and from 69% to about 80% for the bisection task for the two subjects who were trained first with the vernier task, and from 73% to 82% for the bisection task and from 71% to 83% for the vernier task for the other two subjects who started the bisection task first. Subjects' performance did not change significantly in the remaining sessions.

Task switches occurred in blocks 11, 21, 31, 41 and 51. A significant performance drop was evident only at the first task switch, which is true for transitions either from the vernier to the bisection task or vice versa, indicating that the learning was task-specific. Our results for the first two phases of training were in complete agreement with Fahle and Morgan (1996), but we went beyond their results to show the persistence and independence of training in subsequent task alternations.

3.2. New experiment: two tasks with identical input stimuli

Fig. 4 depicts the learning curves for eight subjects. Performance improvement was evident in all subjects and happened mainly in the first 20 blocks (10 for each task). Specifically, performance increased from 71% to 83% in the vernier task and from 71% to 86% in the bisection task for the four subjects who started with the vernier task, and from 70% to 81% in the vernier task and from 71% to 84% in the bisection task for the other four subjects who started with the bisection task. Learning in the last 40 blocks was moderate.

Note that all subjects started training in the two tasks at their respective thresholds, that is, they were expected to perform at 70.7% correct in the beginning of each task if there were no interaction between the two tasks. The observation that they performed around 71% correct in the second training task indicates that training in the first task had essentially no impact on their performance in the second task. Analysis of Variance (ANOVA) revealed no

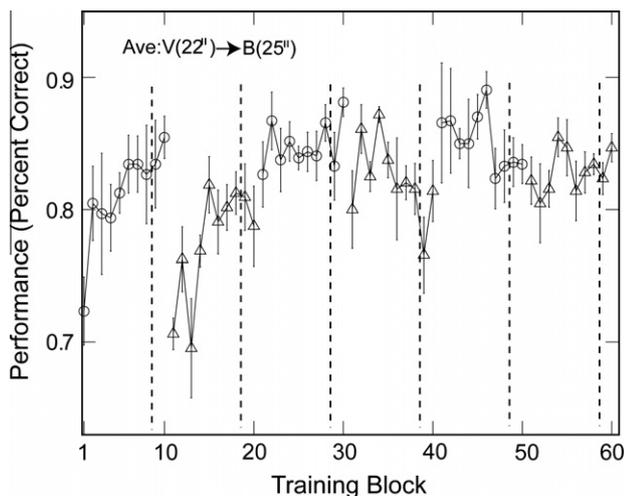


Fig. 3. Average performance of the four observers who replicated Fahle and Morgan (1996). Circles: vernier task; triangles: bisection task. Dashed vertical lines indicate different days. All task switches happened within training sessions.

significant difference between training sequences, for either the vernier ($F(1,180) = 0.45$, $p > 0.50$) or the bisection ($F(1,180) = 2.11$, $p > 0.10$) task, indicating that there was no significant interaction between the two tasks.

Task switches occurred in blocks 11, 21, 31, 41 and 51. A significant performance drop was evident only at the first task switch, which is true for transitions either from vernier to bisection or vice versa, replicating task-specific learning in these more carefully controlled stimuli. Averaged across subjects and training sequences, training improved performance from 70% to 82% for the vernier task, and from 71% to 85% for the bisection task in the first 10 blocks. More practice after the first 10 blocks did not significantly improve subject's performance: the average performance was 83% and 84% correct in the second and third 10 training blocks for the vernier task, and 85% and 85% for the bisection task.

We rearranged the data for the vernier and bisection tasks and averaged them across subjects. Specifically, we put the performance data for the vernier task in blocks 1–10, 21–30, and 41–50, and the performance data for the bisection task in blocks 11–20, 31–40, and 51–60 (Fig. 5). We found that the regression model with the same slope but different Y-axis intercepts ($\alpha_v = \alpha_b$ and $\beta_v \neq \beta_b$; Eqs. (12) and (13)) accounted for 84.0% of the total variance. The quality of the fit was statistically equivalent ($F(1,57) = 1.78$, $p > 0.10$) to that of the most saturated regression model ($\alpha_v \neq \alpha_b$ and $\beta_v \neq \beta_b$; 84.5%) and was superior ($F(1,58) = 5.85$, $p < 0.02$) to its reduced version ($\alpha_v = \alpha_b$ and $\beta_v = \beta_b$; 82.4%). Using a bootstrap procedure, the learning rates were estimated to be 0.09 ± 0.01 and 0.10 ± 0.01 (mean \pm s.e.), for the two tasks respectively, indicating that subjects learned the vernier and bisection tasks at the same rate.

3.3. Model fit

The augmented Hebbian reweighting model (AHRM) was fit to the average data by adjusting five parameters (Table 1), including internal representational noise (σ_1), decision noise of the vernier (σ_{d1}) and bisection tasks (σ_{d2}), learning rate of the vernier and bisection tasks (η), and activation function non-linearity (γ). The AHRM with independently learned weights to decision in the vernier and bisection tasks provided an excellent account of the data. The predicted learning curves of the Hebbian reweighting model are plotted in Fig. 5 along with the behavioral data. Quantitatively, the model accounted for 84.0% of the variance. The pattern of model performance was essentially the same as that of the human observers: In the model, performance improved from 72% to 82% and from 72% to 83% for the vernier and bisection tasks in the first 10 blocks, respectively. More practice yielded mild improvements, reaching performance levels of 85% and 85%, 86% and 87% in the 20th and 30th block for the vernier and bisection tasks, respectively.

The weight dynamics are shown in Fig. 6. The initial weights (± 0.16) carried very little information about where the offset was. With practice, the weights of the different Gaussian blobs (20 channels, see Fig. 2) were modified to embody the statistical structure of the stimulus environment. The most significant weight increase happened in the middle four detectors, from ± 0.16 to ± 0.23 for the vernier task and from ± 0.16 to ± 0.33 for the bisection task; and weights for all other detectors decreased drastically, from ± 0.16 to about ± 0.02 for the vernier task and from ± 0.16 to about ± 0.03 for the bisection task.

4. Discussion

In this paper, we discriminated two hypotheses of perceptual learning, sensory representation enhancement and selective reweighting, by training subjects with two different tasks with

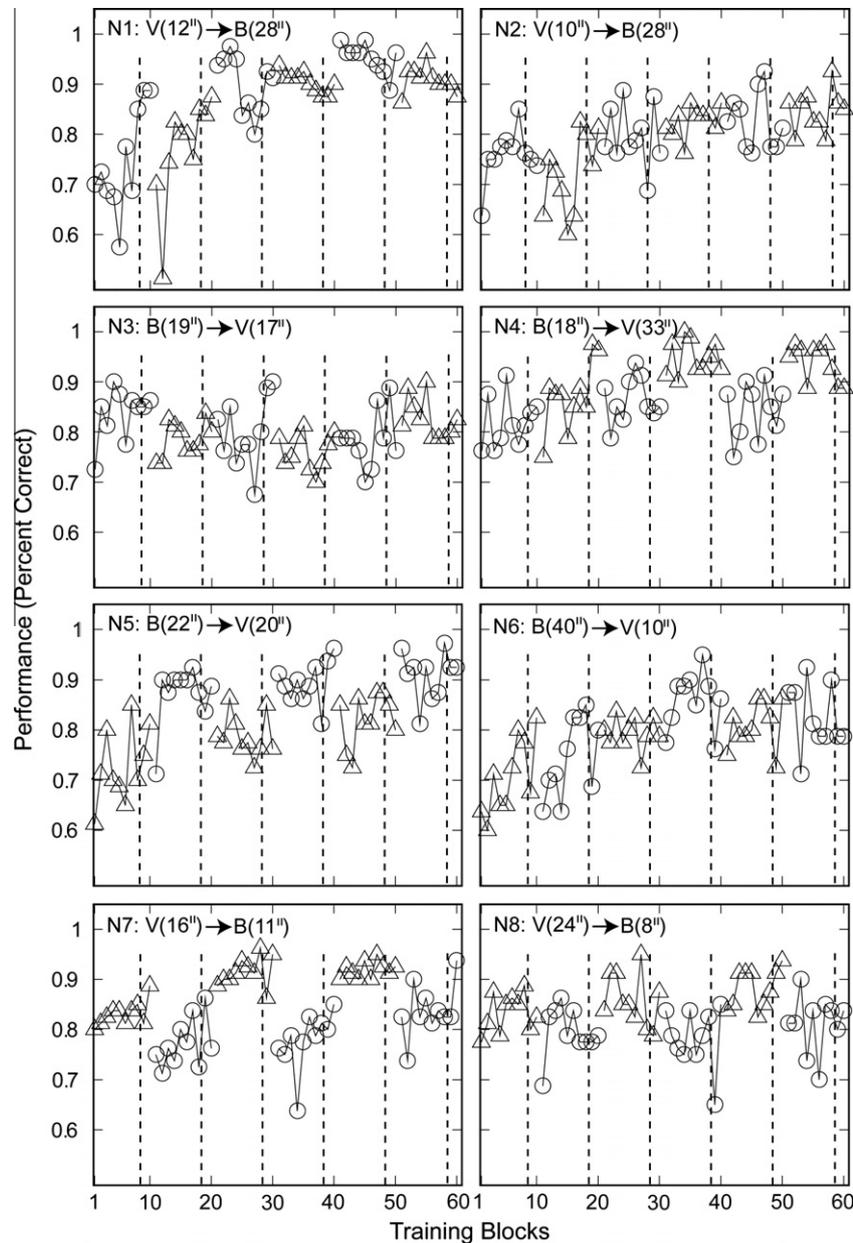


Fig. 4. Learning curves of the eight subjects trained with the tasks of same input stimuli. Circles: vernier task; triangles: bisection task. Dashed vertical lines indicated different days. All task switches happened within training sessions.

the same input stimuli in alternating blocks: If training changes sensory representations, transfer (or interference) must occur since the (changed) sensory representation is shared between the two tasks. If instead, training re-weights a separate set of task connections to decision, performance in the two tasks would be independent. We found that there is no interference in learning the two tasks, supporting the selective reweighting hypothesis.

Perceptual learning in the visual domain has been widely claimed to reflect long-lasting plasticity of sensory representations in early visual cortex (Ahissar & Hochstein, 1996; Crist et al., 1997; Karni & Sagi, 1991; Wilson, 1986), but there is increasing evidence supporting the proposal that the behavioral expression of specificity of perceptual learning in the visual system may reflect reweighted decisions, or changed read-out, from sensory representations (Doshier & Lu, 1998, 1999, 2009; Law & Gold, 2008; Lu, Hua et al., 2010; Mollon & Danilova, 1996). Single cell recording in animals has documented remarkable robustness of early visual repre-

sentations following training (Crist, Li, & Gilbert, 2001; Ghose, Yang, & Maunsell, 2002; Rainer, Lee, & Logothetis, 2004; Yang & Maunsell, 2004; but see Hua et al. (2010)). In this paper, we designed a co-learning paradigm of two tasks with exactly the same inputs (and sensory representations) and found that the two tasks were learned independently, consistent with the selective reweighting theory (Doshier & Lu, 1998, 1999).

The experiments put strong constraints on the loci of perceptual learning in the vernier and bisection tasks – learning must have happened in non-shared pathways of the two tasks. Because the same inputs are used for the two tasks, we can conclude that learning occurred in brain areas after the common sensory representation. The conclusion is based on the almost complete specificity (independence) of the learning of the two tasks. Any transfer or interference between the learning of the two tasks would have suggested changes in the shared representation or overlap in the decision structure.

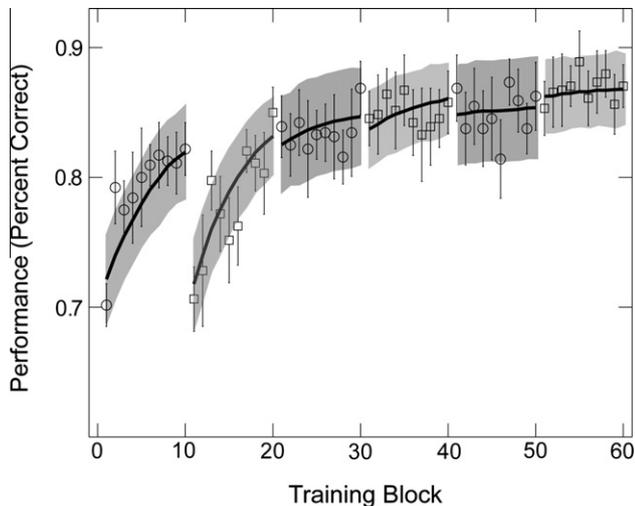


Fig. 5. AHRM model fits to the average behavioral results. For simplicity, the performance data for the vernier task are shown in blocks 1–10, 21–30 and 41–50, and the performance data for bisection task in blocks 11–20, 31–40 and 51–60 for all observers. The points and error bars represent the average performance and the standard error of the mean: circle for the vernier task and square for the bisection task. The solid lines represent performance of the simulated AHRM in the vernier and bisection tasks, respectively. Shaded areas represent ± 2 SD of the mean model performance.

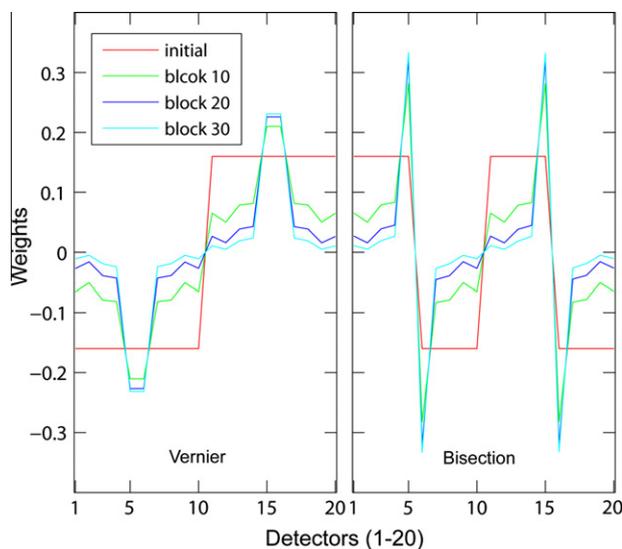


Fig. 6. Weight dynamics of the AHRM. Red line: initial weights before training, which were set at ± 0.16 for both the vernier and bisection tasks; green line: weights after 10 blocks of training; blue line: weights after 20 blocks of training; cyan line: weights after 30 blocks of training. The 20 detectors (10×2 matrix in Fig. 2) were numbered in a column-wise fashion (1–10 for the detectors in the first column; and 11–20 for the detectors in the second column). The system adaptively learns to increase the weights of the most relevant detectors (e.g. detectors 5, 6, 15 and 16) and reduce the contributions from all other detectors to improve its performance.

Because complete specificity between training tasks may be the exception rather than the rule in perceptual learning (Huang et al., 2011; Sagi, 2011; Zhang et al., 2010), our results may be specific to the two tasks used in this study. Moreover, we cannot infer the exact physiological locus/loci of perceptual learning from the results of this study. In our implementation of the AHRM model, the positional information of the stimuli is represented by the outputs of 20 Gaussian detectors (Poggio et al., 1992), rather than the orientation and spatial frequency detectors of the original AHRM. Although one can construct these Gaussian detectors from neurons

in LGN or V1, our analysis does not specify where the sensory representation units reside in the visual pathway.

In this study, most of the performance improvements occurred in the first three blocks of training in each task within a single day; no evidence of consolidation between training days was found. The results cannot rule out the idea that early learning is high level and the learning is projected down into sensory regions only after consolidation (Ahissar & Hochstein, 2004; Censor & Sagi, 2009a), and the idea that different tasks are integrated only during one session before consolidation but not when practiced in different sessions (Censor & Sagi, 2009b; Seitz et al., 2005).

Li, Piech, and Gilbert (2004) used line vernier and line bisection tasks, each with five offset levels in 25 possible stimulus conditions (5×5) to train monkeys, and recorded neuronal responses in the early visual cortex. They found that neurons responded differently to an “identical” stimulus when monkeys performed different tasks, indicating task-specific learning at the neuronal level. Our behavioral results are consistent with theirs in terms of the observed high degree of task-specificity. It should be noted that there were additional task-modulator relations to be learned in their paradigm because monkeys had to learn to focus on the three task-relevant lines (out of five) during each trial. In our paradigm, however, both tasks relied on the same three-dot stimulus. It might be interesting to apply our paradigm in animals and test neuronal responses in different task conditions.

Using a hyperBF (hyper basis function) network of orientation-selective neurons (Weiss, Fahle, & Edelman, 1993) and a supervised learning rule, Sotiropoulos, Seitz, and Series (2011) simulated human performance in a hyperacuity task and found that their simple model handled a variety of phenomena such as disruption of learning and transfer between tasks (Sotiropoulos, Seitz, & Series, 2011). Their model differs from the ARHM in several ways: (1) the Sotiropoulos, Seitz, and Series (2011) model learns in a supervised fashion, while the AHRM is based on an augmented Hebbian learning rule; (2) their model does not include normalization. We have developed a modified ARHM to account for the results from our new paradigm in this study.

While the focus of this paper is on task specificity of perceptual learning, several recent papers have re-examined location specificity of perceptual learning and found that a number of factors in the training procedures, some of those were not obviously related to specificity or transfer of learning, determined the degree of location specificity, including task precision (Jeter et al., 2009), length of training (Jeter et al., 2010), task difficulty (Ahissar & Hochstein, 1997), number of trials (Censor & Sagi, 2009b), and training schedule (Xiao et al., 2008). Xiao et al. (2008) 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. They showed that this additional location training enabled a complete transfer of feature learning (e.g., contrast) to the second location. A rule-based learning theory, consistent with the selective re-weighting hypothesis, has recently been proposed to account for the double-training results (Zhang et al., 2010).

The AHRM and its extensions account for many observations in the literature, including learning in non-stationary background with and without external feedback (Petrov, Doshier, & Lu, 2005, 2006), asymmetrical transfer between training with clear and noisy displays (Lu, Liu, & Doshier, 2010), and the interaction between task difficulty and external feedback (Liu, Lu, & Doshier, 2010). It should be noted that the model has been developed to model perceptual learning in a relatively confined spatial region. Although it has been used to model specificity and transfer of perceptual learning across different contexts, the AHRM needs further development to model specificity and transfer of perceptual

learning in different retinal locations (Doshier et al., 2011; Liu, Lu, & Doshier, 2011).

The current study implies stability of sensory representations, which is at odds with proposed changes in representation units (Bao et al., 2010; Bejjanki et al., 2011; Furmanski, Schluppeck, & Engel, 2004; Hua et al., 2010), and possibly with proposed changes in lateral interactions (Polat & Sagi, 1993) – at least for these hyperacuity tasks. On the other hand, our evidence is silent in relation to proposals for different recurrent networks (Zhaoping, Herzog, & Dayan, 2003) and with perceptual learning at multiple levels of the visual system (Ahissar & Hochstein, 2004). These possibilities and the dependence on tasks remain to be explored.

In summary, the observed pattern of learning in two different tasks with the same stimuli lends further support for the selective re-weighting hypothesis in perceptual learning of vernier and bisection tasks.

Acknowledgments

This research was supported by NEI. There are no competing interests on the research.

References

- Ahissar, M., & Hochstein, S. (1993). Attentional control of early perceptual learning. *Proceedings of the National Academy of Sciences of the United States of America*, 90(12), 5718–5722.
- Ahissar, M., & Hochstein, S. (1996). Learning pop-out detection: Specificities to stimulus characteristics. *Vision Research*, 36(21), 3487–3500.
- Ahissar, M., & Hochstein, S. (1997). Task difficulty and the specificity of perceptual learning. *Nature*, 387(6631), 401–406.
- Ahissar, M., & Hochstein, S. (2004). The reverse hierarchy theory of visual perceptual learning. *Trends in Cognitive Sciences*, 8(10), 457–464.
- Bao, M., Yang, L., Rios, C., He, B., & Engel, S. A. (2010). Perceptual learning increases the strength of the earliest signals in visual cortex. *Journal of Neuroscience*, 30(45), 15080–15084.
- 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.
- Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, 10(4), 433–436.
- Censor, N., & Sagi, D. (2009a). Explaining training induced performance increments and decrements within a unified framework of perceptual learning. *Learning & Perception*, 1, 3–17.
- Censor, N., & Sagi, D. (2009b). Global resistance to local perceptual adaptation in texture discrimination. *Vision Research*, 49(21), 2550–2556.
- 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.
- Crist, R. E., Li, W., & Gilbert, C. D. (2001). Learning to see: Experience and attention in primary visual cortex. *Nature Neuroscience*, 4(5), 519–525.
- Doshier, B. A., Jeter, P. E., Liu, J., & Lu, Z. L. (2011). A multi-location augmented Hebbian reweighting model (m-AHRM) of transfer in perceptual learning (abstract). Vision Science Society: Naples, FL.
- Doshier, B. A., & Lu, Z. L. (1998). Perceptual learning reflects external noise filtering and internal noise reduction through channel reweighting. *Proceedings of the National Academy of Sciences of the United States of America*, 95(23), 13988–13993.
- Doshier, B. A., & Lu, Z. L. (1999). Mechanisms of perceptual learning. *Vision Research*, 39(19), 3197–3221.
- Doshier, B. A., & Lu, Z. L. (2009). Hebbian reweighting on stable representations in perceptual learning. *Learning & Perception*, 1(1), 37–58.
- Fahle, M., & Morgan, M. (1996). No transfer of perceptual learning between similar stimuli in the same retinal position. *Current Biology*, 6(3), 292–297.
- Fine, I., & Jacobs, R. A. (2002). Comparing perceptual learning tasks: A review. *Journal of Vision*, 2(2), 190–203.
- Fiorentini, A., & Berardi, N. (1997). Visual perceptual learning: A sign of neural plasticity at early stages of visual processing. *Archives Italiennes de Biologie*, 135(2), 157–167.
- Furmanski, C. S., Schluppeck, D., & Engel, S. A. (2004). Learning strengthens the response of primary visual cortex to simple patterns. *Current Biology*, 14(7), 573–578.
- Ghose, G. M., Yang, T., & Maunsell, J. H. (2002). Physiological correlates of perceptual learning in monkey V1 and V2. *Journal of Neurophysiology*, 87(4), 1867–1888.
- Gilbert, C. D., Sigman, M., & Crist, R. E. (2001). The neural basis of perceptual learning. *Neuron*, 31(5), 681–697.
- Hua, T., Bao, P., Huang, C. B., Wang, Z., Xu, J., Zhou, Y., et al. (2010). Perceptual learning improves contrast sensitivity of V1 neurons in cats. *Current Biology*, 20(10), 887–894.
- Huang, X., Lu, H., Zhou, Y., & Liu, Z. (2011). General and specific perceptual learning in radial speed discrimination. *Journal of Vision*, 11(4), 7.
- Jeter, P. E., Doshier, B. A., Liu, S. H., & Lu, Z. L. (2010). Specificity of perceptual learning increases with increased training. *Vision Research*, 50(19), 1928–1940.
- Jeter, P. E., Doshier, B. A., Petrov, A., & Lu, Z. L. (2009). Task precision at transfer determines specificity of perceptual learning. *Journal of Vision*, 9(3), 11–13.
- Karni, A., & Sagi, D. (1991). Where practice makes perfect in texture discrimination: Evidence for primary visual cortex plasticity. *Proceedings of the National Academy of Sciences of the United States of America*, 88(11), 4966–4970.
- Karni, A., Tanne, D., Rubenstein, B. S., Askenasy, J. J., & Sagi, D. (1994). Dependence on REM sleep of overnight improvement of a perceptual skill. *Science*, 265(5172), 679–682.
- Law, C. T., & Gold, J. I. (2008). Neural correlates of perceptual learning in a sensory-motor, but not a sensory, cortical area. *Nature Neuroscience*, 11(4), 505–513.
- Li, W., Piech, V., & Gilbert, C. D. (2004). Perceptual learning and top-down influences in primary visual cortex. *Nature Neuroscience*, 7(6), 651–657.
- Liu, J., Lu, Z. L., & Doshier, B. A. (2010). Augmented Hebbian reweighting: Interactions between feedback and training accuracy in perceptual learning. *Journal of Vision*, 10(10), 29.
- Liu, J., Lu, Z. L., & Doshier, B. A. (2011). Multi-location augmented Hebbian re-weighting accounts for transfer of perceptual learning following double training (abstract). Naples, FL: Vision Science Society.
- Liu, Z., & Weinshall, D. (2000). Mechanisms of generalization in perceptual learning. *Vision Research*, 40(1), 97–109.
- Lu, Z. L., & Doshier, B. A. (1999). Characterizing human perceptual inefficiencies with equivalent internal noise. *Journal of the Optical Society of America A: Optics, Image Science, and Vision*, 16(3), 764–778.
- Lu, Z. L., & Doshier, B. A. (2008). Characterizing observers using external noise and observer models: Assessing internal representations with external noise. *Psychological Review*, 115(1), 44–82.
- Lu, Z. L., Hua, T., Huang, C. B., Zhou, Y., & Doshier, B. A. (2010). Visual perceptual learning. *Neurobiology of Learning and Memory*, 95(2), 145–151.
- Lu, Z. L., Liu, J., & Doshier, B. A. (2010). Modeling mechanisms of perceptual learning with augmented Hebbian re-weighting. *Vision Research*, 50(4), 375–390.
- Mollon, J. D., & Danilova, M. V. (1996). Three remarks on perceptual learning. *Spatial Vision*, 10(1), 51–58.
- O'Reilly, R. C., & Munakata, Y. (2000). *Computational explorations in cognitive neuroscience: Understanding the mind by simulating the brain*. Cambridge, MA: MIT Press.
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, 10(4), 437–442.
- Petrov, A. A., Doshier, B. A., & Lu, Z. L. (2005). The dynamics of perceptual learning: An incremental reweighting model. *Psychological Review*, 112(4), 715–743.
- Petrov, A. A., Doshier, B. A., & Lu, Z. L. (2006). Perceptual learning without feedback in non-stationary contexts: Data and model. *Vision Research*, 46(19), 3177–3197.
- Poggio, T., Fahle, M., & Edelman, S. (1992). Fast perceptual learning in visual hyperacuity. *Science*, 256(5059), 1018–1021.
- Polat, U., & Sagi, D. (1993). Lateral interactions between spatial channels: Suppression and facilitation revealed by lateral masking experiments. *Vision Research*, 33(7), 993–999.
- Rainer, G., Lee, H., & Logothetis, N. K. (2004). The effect of learning on the function of monkey extrastriate visual cortex. *PLoS Biology*, 2(2), E44.
- Sagi, D. (2011). Perceptual learning in *Vision Research*. *Vision Research*, 51(13), 1552–1566.
- Schiltz, C., Bodart, J. M., Dubois, S., Dejardin, S., Michel, C., Roucoux, A., et al. (1999). Neuronal mechanisms of perceptual learning: Changes in human brain activity with training in orientation discrimination. *NeuroImage*, 9(1), 46–62.
- Schwartz, S., Maquet, P., & Frith, C. (2002). Neural correlates of perceptual learning: A functional MRI study of visual texture discrimination. *Proceedings of the National Academy of Sciences of the United States of America*, 99(26), 17137–17142.
- Seitz, A. R., Yamagishi, N., Werner, B., Goda, N., Kawato, M., & Watanabe, T. (2005). Task-specific disruption of perceptual learning. *Proceedings of the National Academy of Sciences of the United States of America*, 102(41), 14895–14900.
- Sotiropoulos, G., Seitz, A. R., & Series, P. (2011). Perceptual learning in visual hyperacuity: A reweighting model. *Vision Research*, 51(6), 585–599.
- Weiss, Y., Fahle, M., & Edelman, S. (1993). Models of perceptual learning in vernier hyperacuity. *Neural Computation*, 5, 695–718.
- Wilson, H. R. (1986). Responses of spatial mechanisms can explain hyperacuity. *Vision Research*, 26(3), 453–469.
- 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.
- Yang, T., & Maunsell, J. H. (2004). The effect of perceptual learning on neuronal responses in monkey visual area V4. *Journal of Neuroscience*, 24(7), 1617–1626.
- Yotsumoto, Y., Watanabe, T., & Sasaki, Y. (2008). Different dynamics of performance and brain activation in the time course of perceptual learning. *Neuron*, 57(6), 827–833.
- 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.
- Zhaoping, L., Herzog, M. H., & Dayan, P. (2003). Nonlinear ideal observation and recurrent preprocessing in perceptual learning. *Network*, 14(2), 233–247.