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Perceptual learning of motion direction discrimination in fovea: Separable mechanisms

Zhong-Lin Lu [a,*], Wilson Chu [a], Barbara Anne Dosher [b]

[a] *Laboratory of Brain Processes (LOBES), Departments of Psychology and Biomedical Engineering, and Neuroscience Graduate Program, University of Southern California, Los Angeles, CA 90089-1061, USA*

[b] *Memory, Attention, and Perception (MAP) Laboratory, Department of Cognitive Sciences and Institute of Mathematical Behavioral Sciences, University of California, Irvine, CA 92697-5100, USA*

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Abstract

Dosher and Lu (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.] proposed three mechanisms of perceptual learning: stimulus enhancement, external noise exclusion, and multiplicative noise reduction. In this study, we used pre-training as a manipulation to evaluate the separability of these mechanisms as a key test of the theoretical framework. Observers were trained in identifying the motion direction of a moving sine-wave grating in fovea with varying amount of superimposed external noise across trials, after receiving no pre-training, pre-training in high external noise, or pre-training in zero external noise in the same task. We found: (1) Without pre-training, perceptual learning significantly reduced contrast thresholds by about the same amount across all the external noise levels. (2) Both types of pre-training significantly reduced contrast thresholds in the corresponding conditions. (3) Pre-training in high external noise greatly reduced subsequent learning in high external noise, accounting for 64.6% of the total (pre-training + subsequent) improvements in that condition. On the other hand, the amount of subsequent learning in low external noise conditions was essentially the same as the total (pre-training + subsequent) amount of improvements in high external noise, suggesting that pre-training in high external noise had mostly only improved performance in noisy displays. (4) Pre-training in zero external noise practically eliminated or left very little additional learning in all the external noise conditions. We concluded that the two mechanisms of perceptual learning, stimulus enhancement, and external noise exclusion, can be trained independently in motion direction discrimination in fovea; training in low noise suffices to improve observer performance over all the external noise conditions.

Keywords: Mechanisms of perceptual learning; External noise exclusion; Stimulus enhancement; Internal noise reduction; Masking; Separable mechanisms

1. Introduction

Performance improvements through training or practice have been observed over a wide range of perceptual tasks in adult humans (Ahissar & Hochstein, 1996; Ball & Sekuler, 1982; Beard, Levi, & Reich, 1995; DeValois, 1977; Dosher & Lu, 1998; Dosher & Lu, 1999; Fahle & Edelman, 1993; Fine & Jacobs, 2000; Fiorentini & Berardi, 1980; Fiorentini & Berardi, 1981; Furmanski & Engel, 2000; Karni & Sagi, 1991; Karni & Sagi, 1993; Mayer, 1983; McKee & Westheimer, 1978; Mollon & Danilova, 1996; Ramachandran & Braddick, 1973; Saarinen & Levi, 1995; Sagi & Tanne, 1994; Shiu & Pashler, 1992; Vogels & Orban, 1985). These improvements often exhibit significant specificity to the trained stimuli or tasks (Ahissar & Hochstein, 1996; Ahissar & Hochstein, 1997; Ahissar, Laiwand, Kozminsky, & Hochstein, 1998; Ball & Sekuler, 1987; Berardi & Fiorentini, 1987; Dorais & Sagi, 1997; Fiorentini & Berardi, 1980;Fiorentini & Berardi, 1981; Karni & Sagi, 1993; Liu & Vaina, 1998; Poggio, Fahle, & Edelman, 1992;

* Corresponding author. Fax: +1 213 7469082.
E-mail address: zhonglin@usc.edu (Z.-L. Lu).

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Ramachandran & Braddick, 1973; Rubenstein & Sagi, 1993; Schoups, Vogels, & Orban, 1995; Shiu & Pashler, 1992). Studies on perceptual learning have traditionally investigated transfer or lack of transfer of perceptual learning to modified forms of the same task or to different, related tasks to assess the character and locus of learning. Several recent studies, however, have focused on understanding what is learned, i.e., improvements of the perceptual system during the course of perceptual learning (Chung, Levi, & Tjan, 2005; Dosher & Lu, 1998; Dosher & Lu, 1999; Gold, Bennett, & Sekuler, 1999; Li, Levi, & Klein, 2003; Lu, Chu, Dosher, & Lee, 2005; Lu & Dosher, 2004; Saarinen & Levi, 1995; Tjan, Chung, & Levi, 2002).

In 1998, Dosher and Lu proposed three mechanisms of perceptual learning: a *stimulus enhancement* mechanism that increases the gain of both the signal and the external noise in the stimulus and is associated with reduction of absolute threshold and performance improvements in the presence of no or low external noise (Fig. 1B), an *external noise exclusion* mechanism that optimizes the perceptual template to exclude external noise or distractors and is associated with performance improvements only in the presence of high external noise (Fig. 1C), and an *internal multiplicative noise* (*or gain control*) *reduction* mechanism that increases system response to stimulus contrast and is associated with improvements throughout the full range of external noise (Fig. 1D). A paradigm based on a combination of the external noise method (Ahumada & Watson, 1985; Burgess, Shaw, & Lubin, 1999; Burgess, Wagner, Jennings, & Barlow, 1981; Lu & Dosher, 1999; Nagaraja, 1964; Pelli, 1981;Pelli & Farell, 1999) with measurements of performance at multiple criterion levels (a proxy for full psychometric functions) throughout the course of perceptual learning was also developed to distinguish pure mechanisms and mechanism mixtures (Dosher & Lu, 1999).

The distinction of the three mechanisms of perceptual learning was based upon parallel theoretical and empirical developments in the study of attention (Dosher & Lu, 2000; Lu & Dosher, 1998). The goal was to generate a theoretical framework to accommodate all possible systematic patterns of performance improvements in perceptual learning (Lu & Dosher, 1999). In the domain of visual attention, single mechanisms of stimulus enhancement and template retuning have been observed in different, systematic circumstances [see (Dosher & Lu, 2000a; Lu, Lesmes, & Dosher, 2002) for review]. In the domain of perceptual learning, one key test of the theoretical framework is whether one can empirically separate each of the three mechanisms of perceptual learning within a task domain, and specify the circumstances under which these mechanisms operate.

In the first few studies of perceptual learning based on the external noise approach, including orientation identification and band-pass noise and novel face identification (Gold et al., 1999; Gold, Sekuler, & Bennett, 2004), virtually identical magnitude of performance improvement (contrast threshold reduction) was observed across all external noise levels. Based on the observation of the virtu-

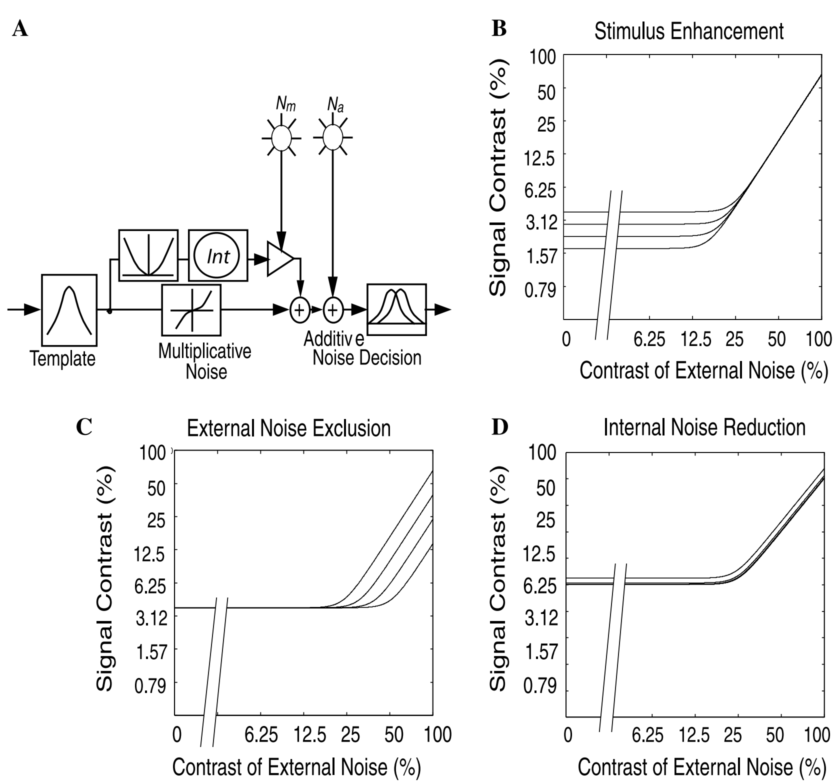

Fig. 1. (A) Perceptual template model. (B–D) Performance signatures of the three mechanisms of perceptual learning.

ally equal magnitudes of contrast threshold reduction in two different criterion performance levels, Dosher and Lu (1998, 1999) concluded that a mixture of stimulus enhancement and template retuning rather than multiplicative noise reduction occurred during perceptual learning in their study. The same data pattern however led Gold et al. (1999, 2004) to a single mechanism of improved efficiency based on a simplified theoretical model of the observer [see (Lu & Dosher, 2004) for detailed discussion]. Although these studies are very interesting (Hurlbert, 2000), they did not provide strong empirical evidence for isolable mechanisms of perceptual learning. On the contrary, one could have concluded from these studies that stimulus enhancement and external noise exclusion are not independently trainable, or alternatively, that a single efficiency mechanism underlies perceptual learning.

Lu and Dosher (2004) provided the first empirical demonstration of a pure, that is, isolated, *external noise exclusion* mechanism of perceptual learning in a psychophysical study. We found that perceptual learning of Gabor orientation identification in fovea showed substantial performance improvements only in high external noise but not in zero or low noise. An isolated *stimulus enhancement* mechanism of perceptual learning has also been demonstrated recently in perceptual learning of auditory amplitude modulation detection (Kong, Lu, Dosher, & Zeng, 2004) and second-order letter identification (Dosher & Lu, 2006). In all these studies, pure mechanisms of perceptual learning occurred "naturally," reflecting the state and plasticity of the perceptual system right before and throughout training.

A stronger test of the separability of the mechanisms is to use explicit experimental manipulations to saturate each individual mechanism and to reveal the other mechanisms in subsequent learning. For stimulus enhancement and template retuning, one way to achieve this is to (1) select a training task and demonstrate that both of these mechanisms occur with roughly equal magnitude "naturally"; (2) pre-train different groups of observers with procedures that exercise one or the other mechanism; and (3) measure the impact of pre-training on mechanisms of subsequent learning. If the mechanisms are completely independent and the pre-training procedures exercise only individual mechanisms, pre-training that exercises one mechanism should only reduce or eliminate that particular mechanism in subsequent learning while leaving potential performance improvements associated with the other mechanism unchanged.

In a recent publication, Dosher and Lu (2005) reported an asymmetric pattern of transfer in perceptual learning of peripheral Gabor orientation identification in clear and noisy displays: training with low noise exemplars transferred to high noise performance, while training with target objects embedded in white external noise did not transfer to low noise performance. They concluded that (1) the two mechanisms of perceptual learning, external noise exclusion and stimulus enhancement, are independent, and (2) different training protocols in zero and high noise allowed different expressions of this independence. Whereas training in high external noise could only optimize the exclusion of external noise, training in zero external noise may be sufficient to substantially optimize the exclusion of external noise as well as enhance the stimulus.

The observed asymmetric pattern of transfer in Dosher and Lu (2005) was highly unexpected but could have major implications for the development of training protocols in the applied field of perceptual learning: that is, training in clear displays may suffice to optimize performance in a range of clear and noisy task environments. It is of paramount importance to test the generality of the results in a wide range of task domains and using different procedures. In this study, we used a different procedure, manipulating the type of pre-training, to investigate the separability of the three mechanisms of perceptual learning in a completely different task domain. We chose sine-wave motion direction identification in fovea as the basic training task because the same task in both fovea and visual periphery was known to have generated essentially equal magnitude of threshold reduction across all the external noise levels (Lu et al., 2005) and because perceptual learning in both zero and high external noise in similar tasks in foveal vision have been documented in the literature (Ball & Sekuler, 1982; Ball & Sekuler, 1987; Liu & Vaina, 1998; Zanker, 1999). Three types of pre-training were administered to three separate groups of observers: no pre-training, pre-training in high external noise, and pre-training in zero external noise. In the subsequent training phase, all observers performed (and practiced) the same task with stimuli embedded in a wide range of external noise levels. Contrast thresholds at two criterion performance levels were measured in ten training sessions. The perceptual template model was then fit to the data to identify mechanisms of perceptual learning. We compared the patterns and mechanisms of perceptual learning after exposure to different pre-training conditions.

2. Methods

2.1. Observers

Ten paid students from the University of Southern California, all with corrected-to-normal vision and naïve to the purpose of the experiment, participated in the study. The participants were randomly assigned into three groups, each of which received a different type of pre-training prior to the same "main" experiment—identify the motion direction of a moving sine-wave grating embedded in (one of) eight levels of external noise. Group I received no pre-training; Group II was pre-trained in the same task with sine-wave gratings embedded in the highest level of external noise.[1] Group III was pre-trained in the task with sine-wave gratings with no external noise. There were three, three, and four observers in the three groups.

[1] A fourth observer (CI) was excluded because an incorrect experimental procedure was inadvertently used on her.

2.2. Apparatus

All the experiments were conducted on a Macintosh Power PC 7500 computer running a version of Psychtoolbox (Brainard, 1997; Pelli, 1997). The computer was equipped with a Nanao Technology Flexscan 6600 monitor with a P4 phosphor, a 640×480 spatial resolution, and a refresh rate of 120 Hz. Fine control of luminance levels was achieved through a special circuit, which combined two eight-bit output of a video card to produce 6144 (12.6 bit) distinct gray levels (Pelli & Zhang, 1991). A lookup table was generated using a psychophysical procedure that provided a linear transformation of pixel value to display luminance (Li, Lu, Xu, Jin, & Zhou, 2003).

All displays were viewed monocularly with natural pupil at a viewing distance of approximately 80 cm in a dimly lit room. A stereoscope rendered the stimuli to one eye and the uniform background to the untested eye (Fig. 2). Observers were instructed to maintain fixation throughout the experiment. A chinrest was used to help observers maintain their head positions.

2.3. Stimulus

Each motion stimulus consisted of five-frames of moving sinusoidal luminance modulations with 90° phase-shifts between successive frames:

$$l(x,y) = l_0\left\{1.0 + c\sin\left[2\pi fx + \frac{\pi}{2}\eta(k-1) + \theta\right]\right\}, \quad k = 1,\ldots,5. \tag{1}$$

where the DC luminance l_0 of the sine-wave gratings was the same as that of the uniform background, set at the middle of the dynamic range of the display (from 1 to 53 cd/m^2). The spatial frequency of the gratings (f) was 3 c/deg. The contrast c was determined by adaptive staircase procedures. The initial phase ($\theta \in [0, 2\pi)$ and the direction of motion ($\eta = \pm 1$) were chosen randomly across trials. The sine-wave gratings were rendered on a 50×50 pixel grid, extending $1.54 \times 1.54°$ of visual angle. They were centered in a $6.34 \times 4.88°$ demarked rectangular box with a central fixation cross (Fig. 2).

For each frame of the sine-wave gratings, an independent external noise image frame of the same size was constructed. Made of 1 by 4 pixels ($0.03 \times 0.12°$), the luminance of each independent patch in the external noise image was drawn independently from a Gaussian distribution with mean l_0 and standard deviation σl_0, where $\sigma \in \{0, 0.02, 0.04, 0.08, 0.12, 0.16, 0.25, 0.33\}$ was determined by the chosen external noise level in a given trial. Because the dynamic range of luminance in the display was $2l_0$, a sample with the maximum standard deviation of $0.33l_0$ conforms reasonably well to a Gaussian distribution.

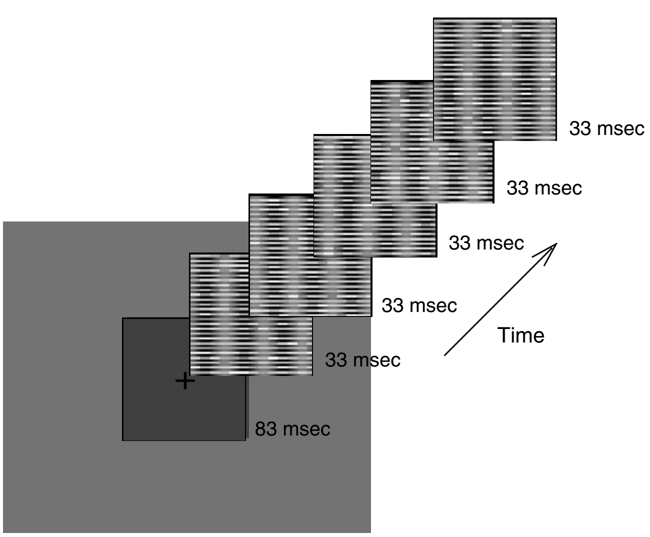

Fig. 2. Display sequence of a five-frame moving sine-wave grating embedded in external noise (via spatial and temporal integration).

Signal and external noise images were combined via spatial and temporal sub-sampling and integration: in a given frame, signal and external noise were displayed in alternating 0.03° rows; across frames, the pixels in a given row were alternately drawn from signal and noise images. Each frame lasted 33 ms. The corresponding motion is therefore at 7.5 Hz—a relatively high temporal frequency at which motion is probably only processed by the first-order motion system (Lu & Sperling, 1995; Lu & Sperling, 2001).

2.4. Design

Observers identified the motion direction of a moving sine-wave grating in each trial. The grating was embedded in eight levels of external noise in the main experiment and only one level of external noise during pre-training. Interleaved adaptive staircase procedures (Levitt, 1971) were used to measure contrast thresholds for motion direction identification at two criterion performance levels in each external noise condition. One staircase procedure (3/1 staircase), aimed at tracking thresholds at 79.3% correct ($d' = 1.634$), decreased signal contrast by 10% ($c_{\text{new}} = 0.90 \times c$) after every three consecutive correct responses and increased signal contrast by 10% ($c_{\text{new}} = 1.10 \times c$) after every incorrect response. The other staircase procedure (2/1 staircase), aimed at tracking thresholds at 70.7% correct ($d' = 1.089$), decreased signal contrast by 10% after two consecutive correct responses and increased signal contrast by 10% after every incorrect response. The staircases were initialized using results from pilot tests in the first session. In all subsequent sessions, the staircases were initialized using results from the last few trials of each staircase in the session immediately preceding them.

Groups II and III received pre-training in the highest and zero external noise conditions, respectively. Thresholds at 70.7 and 79.3% correct were collected using the two staircases with 160 trials per staircase in a single noise condition in each session. Observers ran six sessions on separate days. Each session lasted about 20 min.

In the main experiment, threshold versus contrast of external noise (TvC) functions were sampled at eight external noise levels in all three groups across ten training sessions in separate days. In each session, observer underwent 80 and 60 trials for each of the eight 3/1 and 2/1 staircases, respectively, for a total of 1120 trials. All external noise conditions and staircases were inter-mixed. Each session lasted about 45 min.

2.5. Procedure

Following a key press, each trial started with a fixation display that lasted 83 ms, followed by five signal/external noise image frames, each lasting 33 ms, and the fixation display that lasted until the end of the trial (Fig. 2). Observer responded by pressing different keys on the computer keyboard to indicate different directions of motion. An auditory beep followed each correct response.

3. Results

3.1. Learning curves

For each group, an average threshold versus training session function ("the learning curve") for each external noise condition was calculated by averaging thresholds across observers and criterion performance levels in the corresponding external noise condition for each day of training. A log–log linear regression:

$$\log(c) = B\log(\text{day}) + R \tag{2}$$

was computed for each learning curve using log(day) as the predictor for log(c) using SPSS (SPSS, 1999). This is equivalent to fitting power-law learning functions to the data (Anderson, 1982; Logan, 1988; Suppes & Liang, 1998).

3.1.1. Pre-training learning curves

Learning curves during pre-training are shown in Figs. 3B and D for Groups II and III, respectively. There were a total of $36.9 \pm 5.3\%$ and $44.1 \pm 13.0\%$ threshold reduction for the two groups across the six pre-training sessions, at rates of -0.27 ± 0.06 and -0.33 ± 0.03 log unit of reduction per log unit of session for the two groups (Table 1). All the learning rates are significantly different from zero (no learning; $p < 0.02$). However, the rates and total amounts of learning were not significantly different between the two groups ($p > 0.15$).

3.1.2. Main learning curves

The learning curves from the subsequent main experiment, after pre-training, are shown in Figs. 3A, C, and E for the three groups separately.

For Group I (Fig. 3A), who received no pre-training, significant threshold reduction as a result of training was observed in all the external noise conditions (all $p < 0.01$ except $p < 0.02$ in one condition, Table 1) with an average rate (B) of -0.281 ± 0.058 log unit of threshold reduction per log unit of training session (Eq. (2)) and a total of $40.7 \pm 4.5\%$ threshold reduction over the ten training ses-

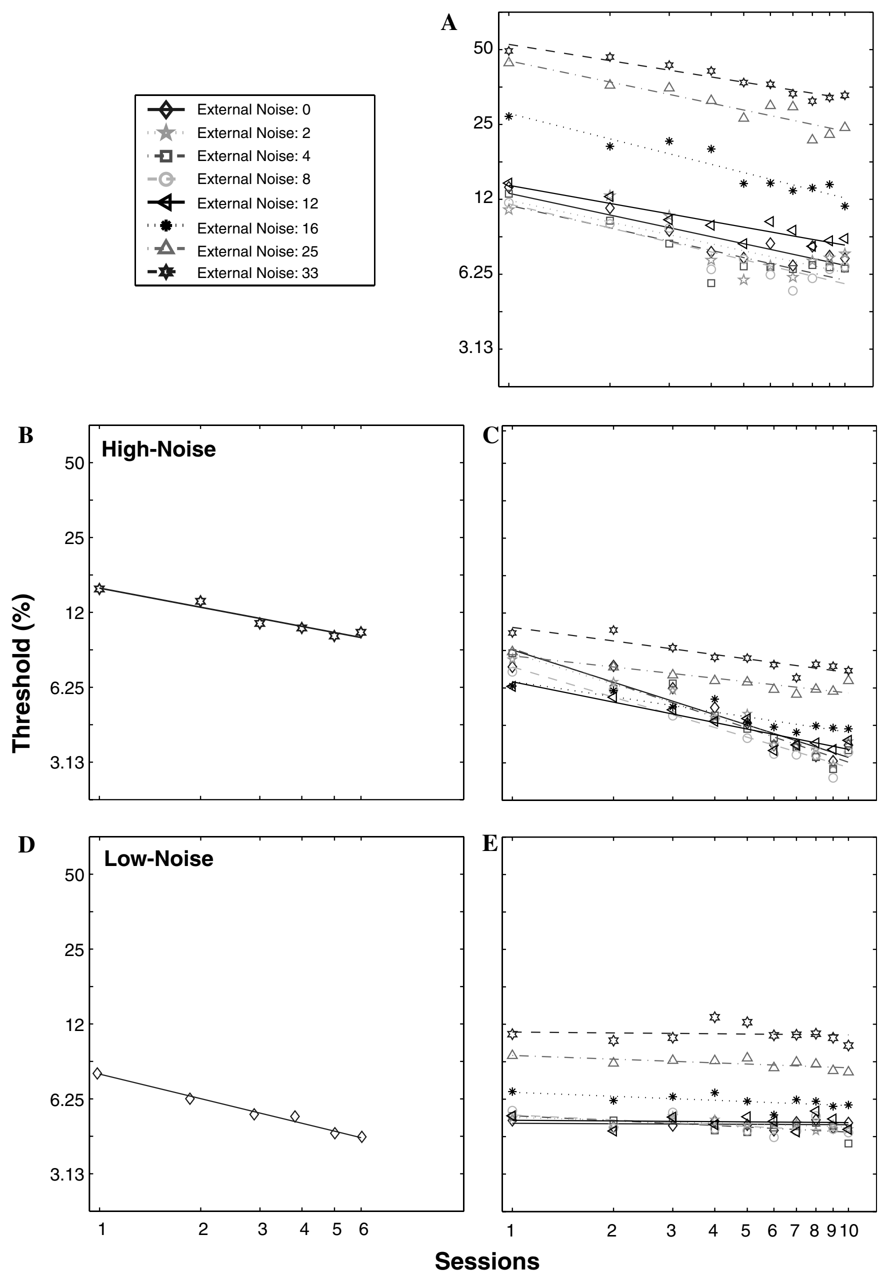

Fig. 3. Learning curves (log threshold contrast versus log training sessions) for the three training groups, averaged over observers and criterion performance levels (70.7 and 79.3%) but presented separately for each external noise level. Straight lines represent best fitting linear regression of the data. (A) Group I: no pre-training but training in all external noise levels. (B and C) Group II: pre-training in high external noise (B) and training in all external noise levels (C). (D and E) Group III: pre-training in zero external noise (D) and training in all external noise levels (E).

Table 1
Regression coefficients

N_{ext}	Experiment 1			Experiment 2			Experiment 3		
	$B \pm SD$	$R \pm SD$	Sig	$B \pm SD$	$R \pm SD$	Sig	$B \pm SD$	$R \pm SD$	Sig
0 or .33	—	—	—	−.27 ± .06	−2.65 ±.12	.020	−.33 ± .06	−3.67 ± .11	.000
.00	−.24 ± .07	−3.03 ± .17	.007	−.54 ± .06	−3.19 ± .14	.000	−.01 ± .02	−4.32 ± .04	.721
.02	−.33 ± .09	−2.82 ± .23	.008	−.51 ± .05	−3.31 ± .13	.000	−.04 ± .02	−4.24 ± .04	.039
.04	−.21 ± .07	−3.25 ± .18	.020	−.53 ± .06	−3.28 ± .14	.000	−.07 ± .03	−4.22 ± .06	.034
.08	−.32 ± .06	−2.97 ± .16	.001	−.51 ± .05	−3.39 ± .12	.000	−.07 ± .03	−4.21 ± .08	.087
.12	−.23 ± .05	−2.89 ± .14	.004	−.44 ± .04	−3.48 ± .11	.000	−.00 ± .03	−4.28 ± .08	.778
.16	−.37 ± .07	−2.07 ± .16	.001	−.33 ± .05	−3.63 ± .13	.000	−.05 ± .02	−3.91 ± .06	.056
.25	−.31 ± .07	−1.66 ± .19	.004	−.33 ± .03	−3.35 ± .06	.000	−.05 ± .02	−3.42 ± .04	.015
.33	−.24 ± .03	−1.43 ± .07	.000	−.29 ± .04	−3.17 ± .09	.000	−.01 ± .04	−3.10 ± .0.1	.763

sions. Virtually identical magnitudes of threshold reduction were observed in the low and high external noise conditions ($p > 0.30$): in the lowest three external noise conditions, thresholds reduced 42.2 ± 2.7%; in the highest two external noise conditions, thresholds reduced by about 40.4 ± 5.5%. A regression analysis on the rate of improvement as a function of log external noise contrast found there was no significant correlation between the rate of improvement and the external noise level ($p > 0.65$). These results are completely consistent with those of Lu et al. (2005).

For Group II (Fig. 3C), who were pre-trained in high external noise, thresholds also reduced significantly in all the external noise conditions ($p < 0.01$). However, the rates and magnitudes of threshold reduction were different in the low and high external noise conditions ($p < 0.001$). In the three lowest external noise conditions, the average rate of threshold reduction was −0.527 ± 0.015 log unit of reduction per log unit of training session with a total of 54.9 ± 1.6% threshold reduction across ten training sessions. In the two highest external noise conditions, the average rate was −0.310 ± 0.028 log unit per log unit of training session with a threshold reduction of 25.5 ± 5.0% (relative to the first session in the main experiment) across the ten training sessions. From the first day of pre-training to the last day of the main experiment, training reduced contrast threshold by a total of 51.8 ± 4.7% in the highest external noise condition, comparable to the amount of learning in the low noise conditions ($p > 0.25$). On the other hand, about 64.6% of the total (pre- and subsequent) improvement in the highest external noise was due to pre-training. The result suggests that pre-training in high external noise had mostly only improved performance in high external noise conditions.

For Group III (Fig. 3E), who were pre-trained in clear displays, no significant ($p > 0.50$) threshold reduction was observed in three external noise conditions ($N_{ext} = .0$, .12, and .33); marginally significant ($0.05 < p < 0.10$) threshold reduction was observed in two external noise conditions ($N_{ext} = .08$ and .16); significant ($p < 0.05$) threshold reduction was observed in the remaining three external noise conditions ($N_{ext} = .02$, .04, and .25). The rate of threshold reduction was minuscule in all the external noise conditions, including those exhibiting significant threshold reduction. The maximum rate was only 0.07 log unit of threshold reduction per log training session with an averaged total threshold reduction of 4.7 ± 3.2% across the ten training sessions.

In summary, in the absence of pre-training (Group I), training in ten sessions reduced contrast thresholds by an approximately equal amount (40.7%) across all the external noise conditions. For Group II, the total amount of improvement in the highest external noise condition (51.8%), including both pre-training and subsequent training in the main experiment, was comparable to that in the low external noise conditions (54.9%) obtained in the subsequent main experiment. Pre-training in high external noise accounted for 64.6% of the total amount of threshold improvements in that condition. It significantly reduced the rate and magnitude of learning in high external noise conditions. Most interestingly, pre-training in zero external noise (Group III) virtually eliminated or left very little further performance improvement in all the external noise conditions.

3.2. TvC functions and PTM modeling

In the main experiment, observers in all three groups identified the direction of sine-wave motion embedded in eight levels of external noise in ten training sessions. Thresholds at two criterion performance levels ($Pc = 70.7\%$ and $Pc = 79.3\%$) were estimated in each external noise condition using adaptive staircase procedures. This design yielded a total of twenty [10 sessions × 2 criterion levels] TVC functions, each sampled at eight external noise levels. The TVC functions for the three groups are shown in Figs. 4–6, pooled over every two sessions.

In all three groups, averaged thresholds across training sessions increased as functions of external noise levels, from 0.088 to 0.255, 0.049 to 0.084, and 0.050 to 0.115, respectively. As expected, the more stringent performance criterion (79.3%) required higher thresholds than the less stringent performance criterion (70.7%). The threshold ratio between the two criterion levels is essentially constant across the eight noise levels and training sessions: mean = 1.36 ± 0.20, 1.32 ± 0.17, and 1.34 ± 0.16, for the three groups respectively. Ratio constancy across external

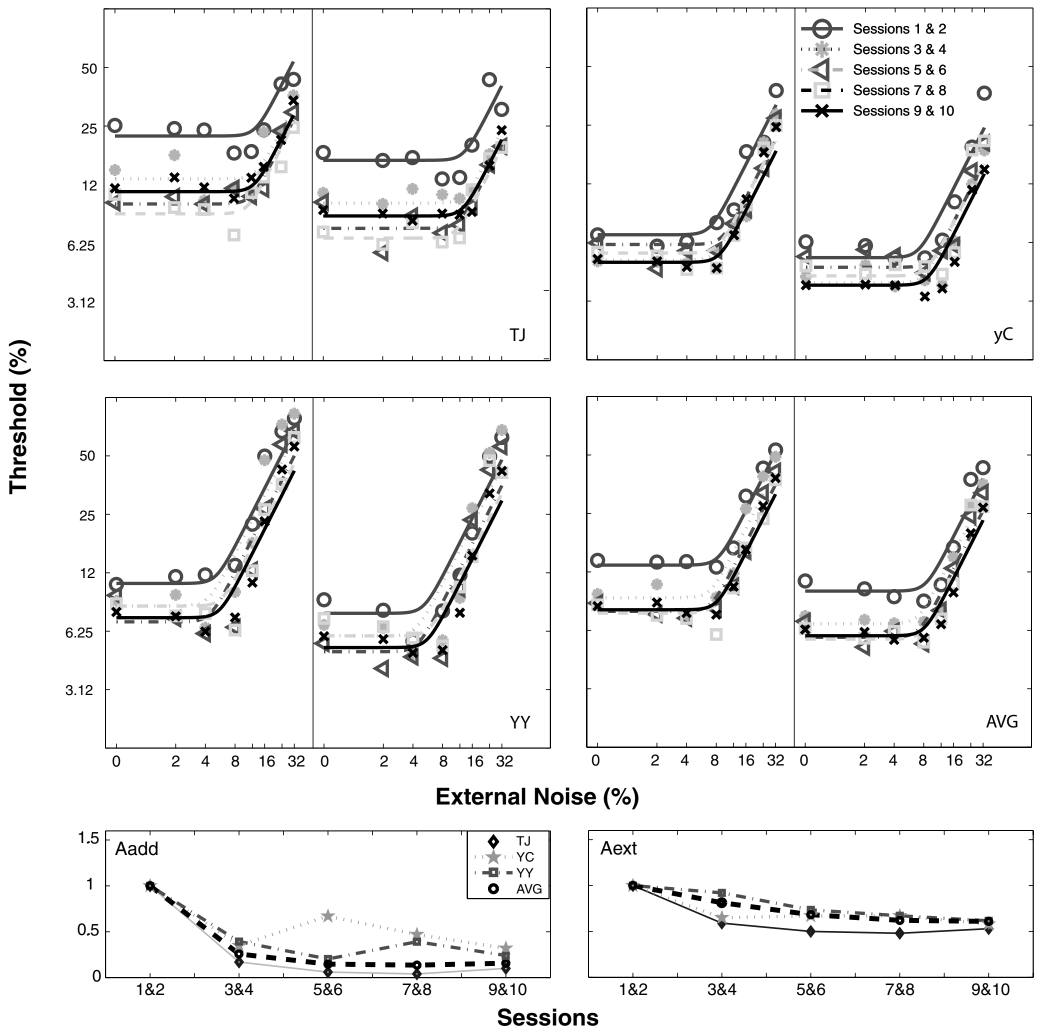

Fig. 4. Experimental results (Group I). Upper panels: threshold versus external noise contrast (TvC) functions at two performance criterion levels (79.3 and 70.7% correct) across ten training sessions for observers TJ, YC, YY, and AVG, sampled at eight external noise levels and averaged over every two training sessions. Lower panels: learning parameter A_{add} [relative amount of internal noise; with $A_{\text{add}}(1 \text{ and } 2) = 1$] and A_{ext} [relative amount of external noise; with $A_{\text{ext}}(1 \text{ and } 2) = 1$] as functions of training session for all the observers.

noise and practice levels indicates that practice did not alter contrast-gain control properties of the perceptual system (Dosher & Lu, 1999; Lu & Dosher, 1999).

TvC functions over training days were fit with the PTM to identify mechanisms of learning during the main experiment (Appendix A) for the three groups separately.

For Group I, performance improved via a mixture of two mechanisms, stimulus enhancement and external noise reduction. For the average observer, the corresponding PTM accounted for 96.9% of the variance with 84% internal additive noise reduction (or an equivalent 525% stimulus enhancement) and 39% external noise exclusion across the training sessions. For all the observers, the model is statistically equivalent to the most saturated model that assumes all three mechanisms of perceptual learning ($p > 0.40$) and is superior to all its subset models ($p < 0.01$) except it is only marginally better than a single stimulus enhancement model for YY, while the model with a single multiplicative noise reduction mechanism of perceptual learning was significantly ($p < 0.001$, TJ, YC, and AVG) or marginally ($p < 0.07$, YY) worse than the most saturated model. The parameters of the best fitting model and the relevant statistics are detailed in Table 2.

For Group II, the performance improvements of the average observer were accounted for 99.3% of the variance with 92% internal additive noise reduction (or an equivalent 1150% stimulus enhancement) and 21% external noise exclusion across the training sessions. For KK and WX, performance improved via a mixture of stimulus enhancement and external noise reduction; the fit was statistically equivalent to the most saturated model that assumes all three mechanisms of perceptual learning ($p > 0.09$ for KK; $p > 0.50$ for WX) and is superior to all its subset models ($p < 0.05$). For MN, performance improved via a single mechanism of stimulus enhancement, i.e., pre-training in high external noise eliminated the mechanism of external noise exclusion in subsequent learning. For all observers in this group, the impact of external noise exclusion was greatly reduced relative to Group I ($p < 0.025$). The relevant statistics are detailed in Table 2.

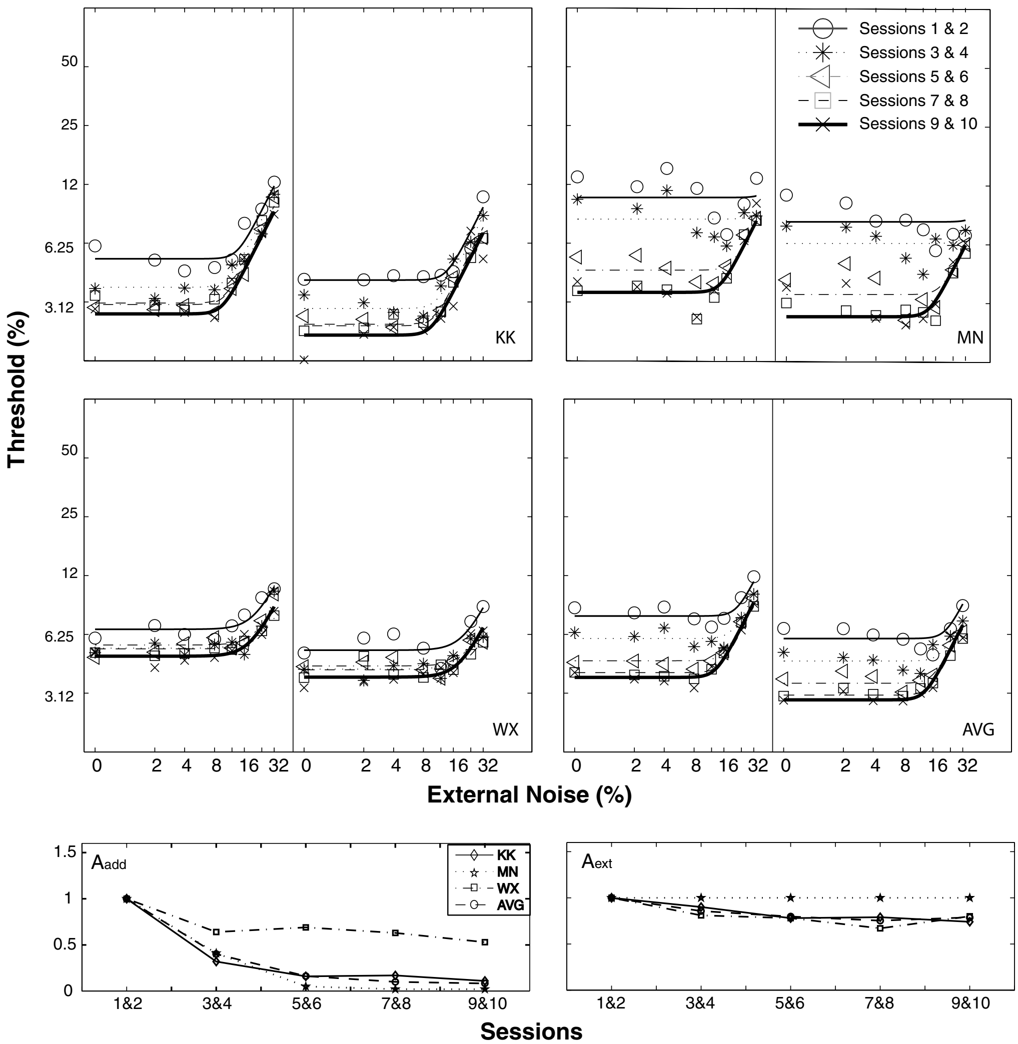

Fig. 5. Experimental results (Group II). Upper panels: threshold versus external noise contrast (TvC) functions at two performance criterion levels (79.3 and 70.7% correct) across ten training sessions for observers KK, MN, WX, and AVG, sampled at eight external noise levels and averaged over every two training sessions. Lower-right panels: learning parameter A_{add} (relative amount of internal noise; with $A_{\mathrm{add}}(1 \text{ and } 2) = 1$) and A_{ext} (relative amount of external noise; with $A_{\mathrm{ext}}(1 \text{ and } 2) = 1$) as functions of training session for all the observers.

For Group III, performance improvements were accounted for by a single mechanism of stimulus enhancement for most observers (IB, SC, and YR), and a mixture of stimulus enhancement and external noise exclusion for JL and the average observer. For the average observer, the two mechanisms model accounted for 99.6% of the variance with 32% internal additive noise reduction (or an equivalent 46.5% stimulus enhancement) and 12% external noise exclusion across the training sessions (Table 2). The magnitudes of stimulus enhancement and external noise exclusion are very much smaller than those in Group I ($p < 0.01$ and $p < 0.025$, respectively).

4. Summary and discussion

Using a motion direction identification task, we investigated the impact of different types of pre-training on the mechanisms of perceptual learning in subsequent training of the same task using three pre-training groups of observers. We first established in Group I that without pre-training, perceptual learning reduced contrast thresholds by a constant 40.7% across all the external noise levels, indicating equal contributions of stimulus enhancement and external noise exclusion during perceptual learning. Observers in Group II were pre-trained in high external noise, resulting in a 36.9% threshold reduction across six pre-training sessions. Subsequent training with the same stimuli embedded in varying amount of external noise reduced contrast threshold by 54.9% in low external noise conditions but only 25.5% (relative to the first session in the main experiment) in high external noise conditions. On the other hand, the total (pre-training + subsequent) amount of learning in the highest external noise (51.8%) was virtually identical to that in the low noise conditions. And pre-training accounted for most of the improvements (64.6%) in the highest external noise condition. Combined with the fact the observers in Group I exhibited essentially the same amount of learning across all external noise levels, the pattern of

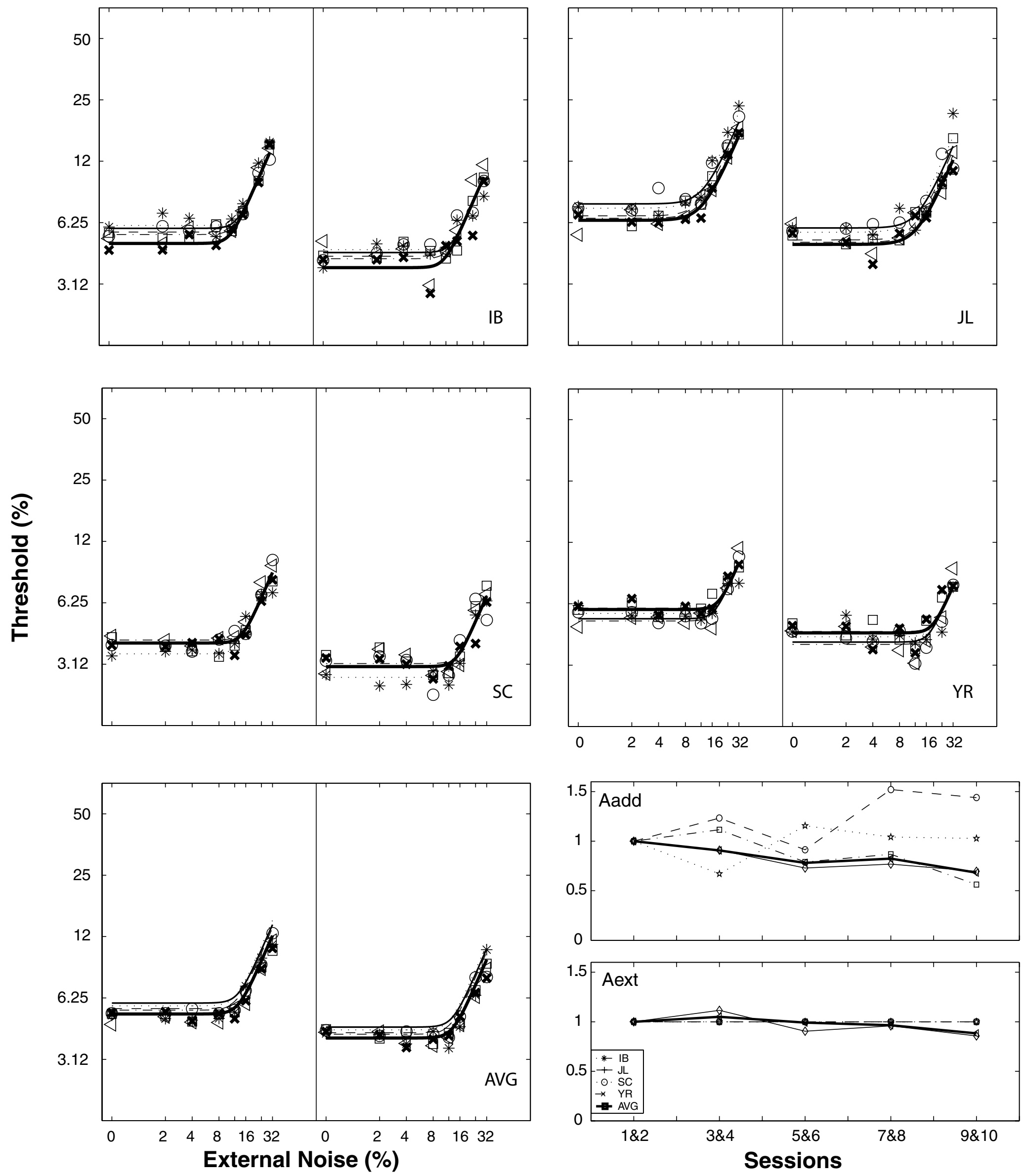

Fig. 6. Experimental results (Group III). Left and upper-right panels: threshold versus external noise contrast (TvC) functions at two performance criterion levels (79.3 and 70.7% correct) across ten training sessions for observers IB, JL, SC, YR, and AVG, sampled at eight external noise levels and averaged over every two training sessions. Lower-right panels: learning parameter A_{add} (relative amount of internal noise; with $A_{\text{add}}(1 \text{ and } 2) = 1$) and A_{ext} (relative amount of external noise; with $A_{\text{ext}}(1 \text{ and } 2) = 1$) as functions of training session for all the observers.

results in Group II suggests that pre-training in high external noise had mostly only improved performance in noisy displays. Consistently, modeling the TvC functions with the PTM found that the impact of external noise exclusion was greatly reduced in Group II. The results suggest that pre-training in high external noise had largely tuned-out external noise exclusion (by 64.6%) in subsequent learning but had left stimulus enhancement in most of its full capacity. In Group III, observers were pre-trained in zero external noise, resulting in a 44.1% threshold reduction across six pre-training sessions. Subsequent training with the same stimuli embedded in varying amount of external noise found only very small though significant amount of additional learning (<5% threshold reduction) in some external noise conditions but no addition learning in other external noise conditions. In other words, pre-training in zero external noise practically eliminated or left very little additional subsequent learning in the same task in all external noise conditions.

The pattern of perceptual learning in Group I—equal threshold reduction across all the external noise levels in identifying motion direction of moving sine-wave gratings—was anticipated, based on results in a prior study using the same task in both fovea and periphery (Lu et al., 2005). The pattern is also similar to that of Dosher and Lu (1998, 1999) and Gold et al. (1999, 2004) using different perceptual tasks. Consistent with Dosher and Lu (1998, 1999), we identified a mixture of stimulus enhance-

Table 2
Parameters of the best fitting PTM's

Parameter	Experiment 1				Experiment 2				Experiment 3				
	TJ	YC	YY	AVG	KK	MN	WX	AVG	IB	JL	SC	YR	AVG
N_{mul}	.55	.54	.58	.56	.52	.55	.31	.53	.55	.43	.54	.54	.52
N_{add}	1.0e−3	1.0e−4	3.7e−5	2.0e−4	1.3e−3	5.7e−2	4.3e−2	5.8e−3	1.1e−03	9.1e−3	1.3e−3	2.4e−3	2.2e−3
β	.91	1.5	.77	.97	3.8	6.0	4.3	4.1	3.5	2.4	5.4	4.8	3.4
γ	3.5	3.5	3.5	3.5	3.4	3.5	2.0	3.5	3.5	2.3	3.5	3.5	3.1
$A_{mul}(2)$	1	1	1	1	1	1	1	1	1	1	1	1	1
$A_{add}(2)$	.17	.35	.39	.26	.32	.41	.64	.40	1.1	.91	.67	1.2	.91
$A_{ext}(2)$	.59	.65	.92	.81	.90	1	.81	.86	1	1.1	1	1	1.1
$A_{mul}(3)$	1	1	1	1	1	1	1	1	1	1	1	1	1
$A_{add}(3)$	.06	.67	.20	.15	.16	.05	.69	.16	.76	.71	1.2	.91	.78
$A_{ext}(3)$	.50	.67	.74	.68	.78	1	.78	.80	1	.90	1	1	.99
$A_{mul}(4)$	1	1	1	1	1	1	1	1	1	1	1	1	1
$A_{add}(4)$	.04	.47	.39	.14	.17	.02	.63	.10	.84	.75	1.04	1.5	.82
$A_{ext}(4)$	.48	.67	.67	.62	.79	1	.67	.75	1	.95	1	1	.96
$A_{mul}(5)$	1	1	1	1	1	1	1	1	1	1	1	1	1
$A_{add}(5)$	.10	.32	.24	.16	.11	.02	.53	.08	.54	.67	1.03	1.4	.68
$A_{ext}(5)$	.53	.58	.62	.61	.74	1	.80	.79	1	.85	1	1	.88
r^2	.963	.965	.918	.969	.990	.969	.991	.993	.985	.985	.988	.986	.996
df	68	68	68	68	68	72	68	68	72	68	72	72	68
$F(4,64)$	1.10^{ns}	1.16^{ns}	0.35^{ns}	0.05^{ns}	2.11^{M}	$.18^{ns}$	$.07^{ns}$	-2.3^{ns}	$.95^{ns}$	$.81^{ns}$	1.27^{ns}	$.231^{ns}$	0.63^{ns}
$F(4,68)$	$9.34^{\#}$	$12.4^{\#}$	4.14^{*}	$15.74^{\#}$	$6.63^{\dagger}$	$.16^{ns}$	3.89^{*}	$9.18^{\#}$	1.60^{ns}	4.19^{*}	1.48^{ns}	1.88^{ns}	2.30^{M}
$F(4,68)$	$35.2^{\#}$	4.62^{*}	1.53^{M}	$12.71^{\#}$	$36.5^{\#}$	$77.7^{\#}$	$13.9^{\#}$	$125.7^{\#}$	3.41^{*}	3.63^{*}	2.25^{M}	$3.03^{\wedge}$	$3.23^{\wedge}$
$F(8,68)$	$28.3^{\#}$	$5.63^{\#}$	$2.76^{\wedge}$	$13.12^{\#}$	$24.9^{\#}$	$41.4^{\#}$	$12.1^{\#}$	$72.73^{\#}$	2.66^{*}	$4.70^{\dagger}$	1.94^{M}	$2.67^{\wedge}$	2.79^{*}

$F(4,64)$: F-statistics resulted from comparing the qualities of the fits of the most saturated three-mechanism PTM to those of the two-mechanism (stimulus enhancement and external noise exclusion) PTM. $F(4,68)$ and $F(4,68)$: F-statistics comparing the quality of the fits of the two-mechanism PTM to those of each of the single-mechanism PTM. $F(8,68)$: F-statistics comparing the quality of the fits of the two-mechanism PTM to those of the most reduced no-learning PTM.

^{M} $p > 0.05$.
^{ns} $p > 0.10$.
$^{\#}$ $p < 0.0001$.
$^{\wedge}$ $p < 0.05$.
† $p < 0.001$.
* $p < 0.01$.

ment and external noise exclusion as the mechanism for perceptual learning. The results of Group I served as an adequate baseline upon which the impact of pre-training can be compared.

The general results from Group II were consistent with our hypothesis that pre-training in high external noise would reduce subsequent performance improvements in high external noise conditions but have little or no impact on the amount of performance improvements in low external noise conditions. Based on the learning curve in the corresponding condition in Group I and the learning curve during pre-training in Group II, both of which saturated by session six, we had expected that the amount of pre-training in high external noise, i.e., 1920 trials in a single external noise condition in six sessions, would have completely eliminated subsequent performance improvement in that condition. Yet, we found that threshold in the two highest external noise conditions was further reduced by about 25.5% (relative to the first session in the main experiment) in subsequent training. This was not due to an increase of threshold in high external noise conditions in the mixed training environment, because the threshold in the end of pre-training and the beginning of subsequent training in the same external noise condition was virtually identical (.104 and .105). The effect might reflect additional learning in this condition in a new learning environment where learning in low external noise conditions further improved the perceptual template.

In the PTM observer framework, three separate mechanisms of perceptual learning, *stimulus enhancement*, *external noise exclusion*, and *internal multiplicative noise* (*or gain control*) *reduction*, have been proposed to accommodate all possible systematic patterns of performance improvements in perceptual learning (Dosher & Lu, 1999). Empirically, pure, isolated mechanisms of stimulus enhancement (Dosher & Lu, 2006; Kong et al., 2004) and external noise exclusion (Lu & Dosher, 2004) have been documented. Prior to this study, we had expected that pre-training in low and high external noise would only reduce the magnitude of performance improvements in corresponding conditions during subsequent training. Even though the pattern of results in Group II (pre-training in high external noise) was consistent with our expectation, that pre-training in zero external noise practically eliminated subsequent learning in all the external noise conditions (Group III) was a complete surprise.

That pre-training in high external noise is only effective in high external noise without impacting learning in low external noise (Group II) completely rules out a single mechanism account of perceptual learning. In fact, any theoretical explanation of Group II results must invoke at least two independent mechanisms, one of which is only effective in high external noise. This dual mechanism account does not however require independent manifestation of the two independent mechanisms in every circumstance—a particular training protocol could in fact train both mechanisms simultaneously and therefore expose both mechanisms together.

We suggest that, in this study, pre-training in high external noise only impacted the external noise external noise mechanism, but pre-training in zero noise impacted both stimulus enhancement and external noise exclusion. In the presence of high external noise, observer's performance is ONLY limited by external noise, not by internal noise. The only way to improve performance is to re-tune the perceptual template to eliminate external noise. That is how observers learned in pre-training and continued to benefit in subsequent learning. In zero external noise, observer's performance is limited by internal additive noise. They did indeed improve their performance via stimulus enhancement during pre-training and continue to benefit in low external noise during subsequent learning. In addition, the observers were also exposed to the signal stimuli and were exercising the perceptual template. We suggest that the exposure to signal stimuli during pre-training in zero external noise condition allowed the observers to re-tune their perceptual templates (Seitz & Watanabe, 2003; Watanabe et al., 2002). Although the retuning did not directly benefit their performance during pre-training, it benefited performance in subsequent testing in high external noise.

The asymmetric effects of pre-training in high and low external noise complement the results of Dosher and Lu (2005), who found a similar asymmetric pattern of transfer in perceptual learning of peripheral Gabor orientation identification in clear and noisy displays: training with low noise exemplars transferred to high noise performance, while training with target objects embedded in white external noise did not transfer to low noise performance. Relatively simple visual stimuli and white external noise were used in Dosher and Lu (2005) and the current study. Both studies suggest that training in clear (low noise) displays may suffice to optimize performance in a range of clear and noisy task environments. In situations in which noise is nonwhite, the noise environment and the optimal perceptual template cannot be known in advance. Training in clear displays should remain useful, but training in the particular kind of nonwhite noise environment may also be necessary to further optimize performance in that environment. Whether the same results will obtain for more complex perceptual tasks needs further experimentation.

In many practical applications, perceptual expertise is required in environments with various degrees of visual noise, such as crowded or camouflaged situations (Parkes, Lund, Angelucci, Solomon, & Morgan, 2001), and alternative sensor environments (Burgess et al., 1999; Sowden, Davies, & Roling, 2000). The results of the current study suggest that it may not be necessary to train the observers in each operating environment. Clear displays may provide the optimal training environment.

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Appendix A

The Perceptual Template Model (Lu & Dosher, 1999) quantitatively models human performance in signal detection and discrimination. In the PTM, perceptual inefficiencies are attributed to three limitations: internal additive noise that is associated with absolute thresholds in perceptual tasks; perceptual templates that is often tuned to a range of stimulus features and often allows unnecessary influence of external noise or distractors on performance; and internal multiplicative noise that is associated with Weber's law behavior of the perceptual system. The basic PTM consists of four parameters in the basic PTM: gain to the signal stimulus (β), exponent of the nonlinear transducer function (γ), internal additive noise (N_{add}), and coefficient of the multiplicative internal noise (N_{mul}). The three mechanisms of perceptual learning were implemented by multiplying the corresponding noise.[2] in the PTM with learning parameters $A_{\text{add}}(t)$, $A_{\text{ext}}(t)$, and $A_{\text{mul}}(t)$ in each training block t, with $A_{\text{add}}(1) = A_{\text{ext}}(1) = A_{\text{mul}}(1) = 1.0$ (Dosher & Lu, 1999; Lu & Dosher, 2004). In the most saturated PTM with all three mechanisms of perceptual learning, thresholds are expressed as functions of external noise by the following equation:

$$c_\tau = \frac{1}{\beta}\left[\frac{(1+(A_{\text{mul}}(t)N_{\text{mul}})^2)(A_{\text{ext}}(t)N_{\text{ext}})^{2\gamma} + (A_{\text{add}}(t)N_{\text{add}})^2}{(1/d'^2 - (A_{\text{mul}}(t)N_{\text{mul}})^2)}\right]^{\frac{1}{2\gamma}}. \tag{A1}$$

All eight possible versions of PTM models, consisting of various combinations of the three mechanisms of perceptual learning, were fit to each set of TvC functions, separated by training and transfer sessions. A least-square minimization procedure based on *fmins* in Matlab 6.5 (Mathworks, 1998) was used to search for the best fitting parameters for each PTM: (1) $\log(c^{\text{theory}})$ was calculated from the model using an initial set of parameters for each external noise condition, performance criterion, and training block; (2) Least-square L was calculated by summing the squared dif-

[2] In the PTM, stimulus enhancement is mathematically equivalent to internal additive noise reduction Lu and Dosher (1998) External noise distinguishes attention mechanisms. *Vision Research, 38* (9), 1183–1198.

ferences $sqdiff = [\log(c^{\text{theory}}) - \log(c)]^2$ across all the conditions; (3) Model parameters were adjusted by *fmins* to search for the minimum L using gradient descend and re-iterating steps (1) and (2). The proportion of variance accounted for by the model form was calculated using the r^2 statistic:

$$r^2 = 1.0 - \frac{\sum[\log(c^{\text{theory}}) - \log(c)]^2}{\sum[\log(c^{\text{theory}}) - \text{mean}(\log(c))]^2}, \tag{A2}$$

where $\sum$ and mean() were over all the conditions.

The quality of the fits of the eight forms of PTM was statistically compared to select the best fitting model for each data set. The best fitting model, statistically equivalent to the fullest yet with minimum number of parameters, identified the mechanism(s) of perceptual learning. When appropriate, F-tests for nested models were used:

$$F(df_1, df_2) = \frac{(r^2_{\text{full}} - r^2_{\text{reduced}})/df_1}{(1 - r^2_{\text{full}})/df_2}, \tag{A3}$$

where $df_1 = k_{\text{full}} - k_{\text{reduced}}$, and $df_2 = N - k_{\text{full}}$. The k's are the number of parameters in each model, and N is the number of predicted data points.

References

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., Laiwand, R., Kozminsky, G., & Hochstein, S. (1998). Learning pop-out detection: Building representations for conflicting target-distractor relationships. *Vision Research, 38*(20), 3095–3107.

Ahumada, A. J., & Watson, A. B. (1985). Equivalent-noise model for contrast detection and discrimination. *Journal of the Optical Society of America A, 2*(7), 1133–1139.

Anderson, J. R. (1982). Acquisition of cognitive skill. *Psychological Review, 89*(4), 369–406.

Ball, K., & Sekuler, R. (1982). A specific and enduring improvement in visual motion discrimination. *Science, 218*(4573), 697–698.

Ball, K., & Sekuler, R. (1987). Direction-specific improvement in motion discrimination. *Vision Research, 27*(6), 953–965.

Beard, B. L., Levi, D. M., & Reich, L. N. (1995). Perceptual learning in parafoveal vision. *Vision Research, 35*(12), 1679–1690.

Berardi, N., & Fiorentini, A. (1987). Interhemispheric transfer of visual information in humans: Spatial characteristics. *Journal of Physiology, 384*, 633–647.

Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision, 10*(4), 433–436.

Burgess, A. E., Shaw, R., & Lubin, J. (1999). Noise in imaging systems and human vision. *Journal of the Optical Society of America a-Optics Image Science and Vision, 16*(3), 618.

Burgess, A. E., Wagner, R. F., Jennings, R. J., & Barlow, H. B. (1981). Efficiency of human visual signal discrimination. *Science, 214*(4516), 93–94.

Chung, S. T. L., Levi, D. M., & Tjan, B. S. (2005). Learning letter identification in peripheral vision. *Vision Research, 45*, 1399–1412.

DeValois, K. (1977). Spatial frequency adaptation can enhance contrast sensitivity. *Vision Research, 17*, 1057–1065.

Dorais, A., & Sagi, D. (1997). Contrast masking effects change with practice. *Vision Research, 37*(13), 1725–1733.

Dosher, B., & Lu, Z.-L. (2006). Level and mechanisms of perceptual learning: Learning first-order luminance and second-order texture objects. *Vision Research, 46*(12), 1996–2007.

Dosher, 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.

Dosher, B. A., & Lu, Z.-L. (1999). Mechanisms of perceptual learning. *Vision Research, 39*(19), 3197–3221.

Dosher, B. A., & Lu, Z.-L. (2000). Noise exclusion in spatial attention. *Psychological Science, 11*(2), 139–146.

Dosher, B. A., & Lu, Z.-L. (2000a). Mechanism of perceptual attention in precuing of location. *Vision Research*(40), 1269–1292.

Dosher, B. A., & Lu, Z.-L. (2005). Perceptual learning in clear displays optimizes perceptual expertise: Learning the limiting process. *Proceedings of the National Academy of Sciences of the United States of America, 102*(14), 5286–5290.

Fahle, M., & Edelman, S. (1993). Long-term learning in vernier acuity: Effects of stimulus orientation, range and of feedback. *Vision Research, 33*(3), 397–412.

Fine, I., & Jacobs, R. A. (2000). Perceptual learning for a pattern discrimination task. *Vision Research, 40*(23), 3209–3230.

Fiorentini, A., & Berardi, N. (1980). Perceptual learning specific for orientation and spatial frequency. *Nature, 287*(5777), 43–44.

Fiorentini, A., & Berardi, N. (1981). Learning in grating waveform discrimination: Specificity for orientation and spatial frequency. *Vision Research, 21*(7), 1149–1158.

Furmanski, C. S., & Engel, S. A. (2000). Perceptual learning in object recognition: Object specificity and size invariance. *Vision Research, 40*(5), 473–484.

Gold, J., Bennett, P. J., & Sekuler, A. B. (1999). Signal but not noise changes with perceptual learning. *Nature, 402*(6758), 176–178.

Gold, J., Sekuler, A. B., & Bennett, P. J. (2004). Characterizing perceptual learning with external noise. *Cognitive Science, 28*(2), 167–207.

Hurlbert, A. (2000). Visual perception: Learning to see through noise. *Current Biology, 10*, R231–R233.

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., & Sagi, D. (1993). The time course of learning a visual skill. *Nature, 365*(6443), 250–252.

Kong, Y.-Y., Lu, Z.-L., Dosher, B. A., & Zeng, F.-G. (2004). Mechanisms of perceptual learning in amplitude modulation detection. Available from: Association for Research in Otolaryngology Mid-Winter Meeting, <http://www.aro.org/archives/2004/2004_1294.html>.

Levitt, H. (1971). Transformed up-down methods in psychoacoustics. *Journal of the Acoustical Society of America, 49*(2Pt. 2), 467–477.

Li, R. W., Levi, D. M., & Klein, S. A. (2003). Perceptual learning improves efficiency by re-tuning the "template" for position discrimination. *Nature Neuroscience, 7*, 178–183.

Li, X., Lu, Z.-L., Xu, P., Jin, J., & Zhou, Y. (2003). Generating high gray-level resolution monochrome displays with conventional computer graphics cards and color monitors. *Journal of Neuroscience Methods, 130*, 9–18.

Liu, Z., & Vaina, L. M. (1998). Simultaneous learning of motion discrimination in two directions. *Cognitive Brain Research, 6*(4), 347–349.

Logan, G. D. (1988). Toward an instance theory of automatization. *Psychological Review, 95*(4), 492–527.

Lu, Z.-L., Chu, W., Dosher, B., & Lee, S. (2005). Independent perceptual learning in monocular and binocular motion systems. *Proceedings of the National Academy of Sciences of the United States of America, 102*, 5624–5629.

Lu, Z.-L., & Dosher, B. A. (1998). External noise distinguishes attention mechanisms. *Vision Research, 38*(9), 1183–1198.

Lu, Z.-L., & Dosher, 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., & Dosher, B. A. (2004). Perceptual learning retunes the perceptual template in foveal orientation identification. *Journal of Vision, 4*, 44–56.

Lu, Z.-L., Lesmes, L. A., & Dosher, B. A. (2002). Spatial attention excludes external noise at the target location. *Journal of Vision, 2*(4), 312–323.

Lu, Z.-L., & Sperling, G. (1995). The functional architecture of human visual motion perception. *Vision Research, 35*(19), 2697–2722.

Lu, Z.-L., & Sperling, G. (2001). Three-systems theory of human visual motion perception: Review and update. *Journal of the Optical Society of America a-Optics Image Science and Vision, 18*(9), 2331–2370.

Mathworks, I. (1998). Matlab, 5.2.

Mayer, M. (1983). Practice improves adults' sensitivity to diagonals. *Vision Research, 23*, 547–550.

McKee, S. P., & Westheimer, G. (1978). Improvement in vernier acuity with practice. *Perception & Psychophysics, 24*(3), 258–262.

Mollon, J. D., & Danilova, M. V. (1996). Three remarks on perceptual learning. *Spatial Vision, 10*(1), 51–58.

Nagaraja, N. S. (1964). Effect of luminance noise on contrast thresholds. *Journal of the Optical Society of America, 54*(7), 950–955.

Parkes, L., Lund, J., Angelucci, A., Solomon, J. A., & Morgan, M. (2001). Compulsory averaging of crowded orientation signals in human vision. *Nature Neuroscience, 4*(7), 739–744.

Pelli, D. G. (1981). Effects of visual noise. PhD dissertation, University of Cambridge, Cambridge, England.

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision, 10*(4), 437–442.

Pelli, D. G., & Farell, B. (1999). Why use noise? *Journal of the Optical Society of America A, 16*(3), 647–653.

Pelli, D. G., & Zhang, L. (1991). Accurate control of contrast on microcomputer displays. *Vision Research, 31*, 1337–1350.

Poggio, T., Fahle, M., & Edelman, S. (1992). Fast perceptual learning in visual hyperacuity. *Science, 256*(5059), 1018–1021.

Ramachandran, V. S., & Braddick, O. (1973). Orientation-specific learning in stereopsis. *Perception, 2*(3), 371–376.

Rubenstein, B. S., & Sagi, D. (1993). Effects of foreground scale in texture discrimination tasks: Performance in size, shape, and content specific. *Spatial Vision, 7*(4), 293–310.

Saarinen, J., & Levi, D. M. (1995). Perceptual learning in vernier acuity: What is learned? *Vision Research, 35*(4), 519–527.

Sagi, D., & Tanne, D. (1994). Perceptual-Learning—Learning to See. *Current Opinion in Neurobiology, 4*(2), 195–199.

Schoups, A. A., Vogels, R., & Orban, G. A. (1995). Human perceptual learning in identifying the oblique orientation: Retinotopy, orientation specificity and monocularity. *Journal of Physiology, 483*, 797–810.

Seitz, A. R., & Watanabe, T. (2003). Is subliminal learning really passive? *Nature, 422*(6927), 36.

Shiu, L.-p., & Pashler, H. (1992). Improvement in line orientation discrimination is retinally local but dependent on cognitive set. *Perception & Psychophysics, 52*(5), 582–588.

Sowden, P. T., Davies, I. R. L., & Roling, P. (2000). Perceptual learning of the detection of features in X-ray images: A functional role for improvement in adults' visual sensitivity. *Journal of Experimental Psychology: Human Perception & Performance, 26*, 379–390.

SPSS, I. (1999). SPSS for Windows. (Chicago, Illinois).

Suppes, P., & Liang, L. (1998). Concept learning rates and transfer performance of several multivariate neural network models. In C. Dowling, F. S. Roberts, & P. Theuns (Eds.), *Recent Progress in Mathematical Psychology*. Hillsdale, NJ: Lawrence Erlbaum Assoc..

Tjan, B. S., Chung, S., Levi, D. (2002). Limitation of ideal-observer analysis in understanding perceptual learning. Twenty-seventh annual interdisciplinary conference (Jackson Hole, Wyoming. http://aris.ss.uci.edu/HIPLab/AIC/abs.aic02_abc.htm.).

Vogels, R., & Orban, G. A. (1985). The effect of practice on the oblique effect in line orientation judgments. *Vision Research, 25*(11), 1679–1687.

Watanabe, T., Nanez, J. E. S., Koyama, S., Mukai, I., Liederman, J., & Sasaki, Y. (2002). Greater plasticity in lower-level than higher-level visual motion processing in a passive perceptual learning task. *Nature Neuroscience, 5*(10), 1003–1009.

Zanker, J. M. (1999). Perceptual learning in primary and secondary motion vision. *Vision Research, 39*(7), 1293–1304.