

Perceptual learning retunes the perceptual template in foveal orientation identification

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What is learned during perceptual learning? We address this question by analyzing how perceptual inefficiencies improve over the course of perceptual learning (Doshier & Lu, 1998). Systematic measurements of human performance as a function of both the amount of external noise added to the signal stimulus and the length of training received by the observers enable us to track changes of the characteristics of the perceptual system (e.g., internal noise[s] and efficiency of the perceptual template) as perceptual learning progresses, and, therefore, identifies the mechanism(s) underlying the observed performance improvements. Two different observer models, the linear amplifier model (LAM) and the perceptual template model (PTM), however, have led to two very different theories of learning mechanisms. Here we demonstrate the failure of an LAM-based prediction – that the magnitude of learning-induced threshold reduction in high external noise must be less or equal to that in low external noise. In Experiment 1, perceptual learning of Gabor orientation identification in fovea showed substantial performance improvements only in high external noise but not in zero or low noise. The LAM-based model was “forced” to account for the data with a combination of improved calculation efficiency and (paradoxical) compensatory increases of the equivalent internal noise. Based on the PTM framework, we conclude that perceptual learning in this task involved learning how to better exclude external noise, reflecting retuning of the perceptual template. The data provide the first empirical demonstration of an isolable mechanism of perceptual learning. This learning completely transferred to a different visual scale in a second experiment.

Keywords: perceptual learning, linear amplifier model, perceptual template model, calculation efficiency, external noise exclusion, stimulus enhancement, internal noise reduction

Introduction

Perceptual learning – improvements in performance with training or practice – has been demonstrated in adult human observers in a wide range of perceptual tasks (Ahissar & Hochstein, 1996; Ball & Sekuler, 1982; Beard, Levi, & Reich, 1995; DeValois, 1977; Doshier & Lu, 1998; Doshier & 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). Most studies on perceptual learning have investigated transfer or lack of transfer of perceptual learning to modified forms of the same task or to different, related 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; Ramachandran & Braddick, 1973; Rubenstein & Sagi, 1993; Schoups, Vogels, & Orban, 1995; Shiu & Pashler, 1992). These studies do not directly assess task-

relevant changes to the perceptual system during learning itself; rather, they assess the generalizability of perceptual learning at the end of training or practice with important implications for the character and locus of learning.

But, how does the perceptual system change during perceptual learning? What underlies the improved perceptual performance as a result of practice or training? First investigated by Saarinen and Levi (1995) in perceptual learning of a Vernier task, the mechanisms of perceptual learning have been the focus of a number of recent studies (Chung & Tjan, & Levi, 2001; Doshier & Lu, 1998; Doshier & Lu, 1999; Gold, Bennett, & Sekuler, 1999; Li, Levi & Klein, 2003; Tjan, Chung, & Levi, 2002). Using the external noise approach (Doshier & Lu, 1998; Lu & Doshier, 1998; Lu & Doshier, 1999), these studies directly evaluate the mechanisms underlying performance improvements throughout perceptual learning by analyzing the inefficiencies of the perceptual system over the course of practice.

Originally developed by electrical engineers in analyzing noisy amplifiers, the external noise method has become an important tool widely used to characterize and analyze inefficiencies of the perceptual system (Ahumada & Watson, 1985; Burgess, Shaw, & Lubin, 1999; Burgess, Wagner, Jennings, & Barlow, 1981; Lu & Doshier, 1999; Nagaraja, 1964; Pelli, 1981; Pelli & Farell, 1999). In a typical

application, the threshold — signal stimulus energy required for an observer to achieve a given performance level — is measured as a function of the contrast of external noise (the “TVC” function). The method quantitatively assays perceptual inefficiencies in terms of equivalent internal noise(s) and efficiency of the perceptual template. By measuring TVC functions over the course of perceptual learning, the external noise approach to perceptual learning tracks changes of the characteristics of the perceptual system (e.g., internal noise[s] and efficiency of the perceptual template) as perceptual learning progresses and therefore identifies the mechanism(s) underlying the observed performance improvements (Doshier & Lu, 1998, 1999).

In a previous application of the external noise approach, Doshier and Lu (1998, 1999) found that perceptual learning improved performance (reduced contrast thresholds) at all levels of external noise in an orientation identification task in visual periphery. Detailed statistical analyses suggested that although performance improvements in zero and high external noise co-occurred, the magnitudes of these separate improvements were only partially, not perfectly, coupled. Using a theoretical framework based on the perceptual template model (PTM) of a human observer (Lu & Doshier, 1999), Doshier and Lu (1998, 1999) identified a mixture of stimulus enhancement and external noise exclusion (see below) as the mechanism of perceptual learning (Doshier & Lu, 1998; Doshier & Lu, 1999). The data pattern observed by Doshier and Lu (1998, 1999), reduction of contrast threshold throughout an entire range of external noise levels, was later replicated by Gold et al. (1999) using the same external noise approach in two different tasks: band-pass noise and novel face identification. Although the data patterns were identical, Gold et al. (1999) concluded that perceptual learning enhances processing efficiency only for the signal stimulus, a very different conclusion from Doshier and Lu (1998, 1999).

The two drastically different theoretical interpretations of the same data pattern stem from two different models of the human observer, the linear amplifier model (LAM) in Gold et al. (1999) and the perceptual template model (PTM) in Doshier and Lu (1998, 1999). Although it has been frequently shown that LAM is an inadequate observer model for human performance (Burgess & Colborne, 1988; Chung & Tjan, & Levi, 2001; Eckstein, Ahumada, & Watson, 1997; Lu & Doshier, 2002a; Lu & Doshier, 1999; Pelli, 1985; Tjan et al., 2002), the LAM-based efficiency-improvement account of perceptual learning nonetheless has been adopted by some researchers because (1) it requires less systematic data to specify, and (2) it can provide an adequate description of TVC functions at a single performance level. In contrast, although the PTM requires slightly more data to specify, the PTM with a single set of parameters has been shown to coherently account for human performance over a wide range of performance levels or the full psychometric functions (Lu & Doshier, 1999; Lu & Doshier, 2001); the PTM-based accounts of performance improvements in perceptual learning provide very strong

constraints on the magnitudes of perceptual learning at multiple performance levels.

The ability of the PTM to account for performance at different criterion performance levels, and hence the psychometric function, with a single consistent set of parameters is by itself an important advantage. However the choice of model framework — LAM or PTM — also has significant substantial consequences in interpretation of the underlying mechanisms of perceptual learning. Attributing perceptual learning to improved-processing efficiency in a LAM leads to very strong predictive constraints on the relative magnitudes of perceptual learning in high and low external noise levels based on improved calculation efficiency. In contrast, the PTM accommodates independent mechanisms of expressions of perceptual learning in high and low external noise levels.

Detailed theoretical analyses of various external noise methods, observer models including the LAM and the PTM, and theoretical accounts of perceptual learning and attention based on these methods and models have been presented in conferences (Lu & Doshier, 2002a; Lu & Doshier, 2002b) and are in preparation. In this study, we investigate one theoretical constraint for the LAM-based efficiency account of perceptual learning to be parsimonious: magnitude of threshold reduction in low external noise cannot be less than that in high external noise.

We begin by reviewing the LAM, the PTM, and the associated theoretical framework for interpreting the effects of perceptual learning in external noise, as well as the empirical literature on the relationship between learning magnitude and external noise level.

The LAM and the efficiency account of perceptual learning

The LAM (Figure 1a) models the human observer in analogy to a noisy linear amplifier, consisting of a noise-free linear amplification with perceptual or calculation efficiency E , an equivalent additive internal noise N_{eq} , and a decision stage (Ahumada & Watson, 1985; Barlow, 1956; Burgess et al., 1981; Nagaraja, 1964; Pelli, 1981). The concept of perceptual or calculation efficiency is not well understood; however, it is usually interpreted as a reflection of the ability of the observer to utilize sensory information. The equivalent additive noise determines the absolute threshold for the observer.

For a signal stimulus embedded in Gaussian external noise with SD N_{ext} , the LAM predicts that the threshold c at a given performance level τ (e.g., 70.7% correct) as

$$c_{\tau}(N_{ext}) = \sqrt{\frac{N_{eq}^2 + N_{ext}^2}{E_{\tau}}} \quad (1)$$

Note that the calculation efficiency E_{τ} in Equation 1 depends on the performance level upon which threshold is defined. Whereas Equation 1 often provides excellent accounts of psychophysical data at a single performance level

in a wide range of perceptual tasks (for a review, see Burgess et al., 1999), it in general fails to account for human behavior at multiple performance levels, even with a reasonable elaboration that relates E_τ to the corresponding performance levels (Lu & Doshier, 1999).

Because the LAM consists of two parameters, the equivalent additive internal noise (N_{eq}) and the calculation efficiency (E_c), there are essentially two possible ways perceptual learning can improve the performance (reducing thresholds) of the model: (1) increasing calculation efficiency, which results in threshold reduction with equal magnitude (in log) across the full range of external noise levels (Figure 1b), and/or (2) reducing equivalent internal noise, which results in threshold reduction restricted in low external noise conditions (Figure 1c). Therefore, a “pure” efficiency account of perceptual learning (e.g., Gold et al., 1999) predicts perceptual improvements with equal magnitude across all the external noise levels, a prediction rejected by Doshier and Lu (1999).

Here we focus on another theoretical constraint placed by the LAM-based account of perceptual learning – the magnitude of threshold reduction as a result of perceptual learning in high external noise should be less or equal to that in low external noise (Figure 1d). This constraint follows directly from the model prediction that efficiency improvements reduce thresholds with equal magnitude across all the noise levels and internal noise reduction reduces thresholds only in low external noise levels. Therefore, any mixture of the two mechanisms should produce equal or larger threshold reduction in low external noise. If threshold reduction with larger magnitude in high external noise were observed, the LAM-based theory would be “forced” to generate an apparently paradoxical account: perceptual

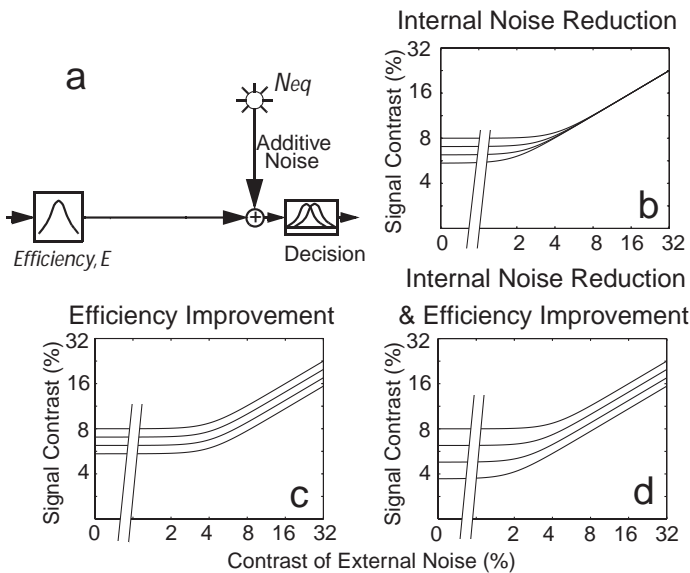


Figure 1. Linear amplifier model (a) and performance signatures of the two mechanisms (b and c) of perceptual learning and their mixture (d).

learning improves calculation efficiency yet increases (disimproves) additive internal noise. Though mathematically possible, such an account of perceptual learning would, however, render the theory much less parsimonious, and additionally would require an explanation of why practice increases the level of internal additive noise.

The PTM and three mechanisms of perceptual learning

The PTM (Lu & Doshier, 1999) attributes perceptual inefficiencies to three limitations: internal additive noise sets the absolute thresholds for perceptual tasks; perceptual templates, often not perfectly matched to the signal in the stimulus, allow unnecessary influence of external noise or distractors on performance; and internal multiplicative noise that increases with input stimulus energy diminishes the benefit from increasing stimulus contrast and therefore predicts Weber’s Law behavior. A PTM consists of five components (Figure 2a): (1) a perceptual template, (2) a nonlinear transducer function, $\|\bullet\|^2$, (3) a multiplicative Gaussian internal noise whose SD is proportional (with a factor of N_{mul}) to the total energy in the stimulus after the nonlinear transformation, (4) an additive internal noise whose amplitude (N_{add}) is independent of the stimulus strength, and (5) a decision process (see Lu & Doshier, 1999, for the formal development and quantitative tests for the form of the PTM model). In the PTM, threshold signal contrast at a particular performance level (i.e., d') is expressed as a function of external noise contrast N_{ext} :

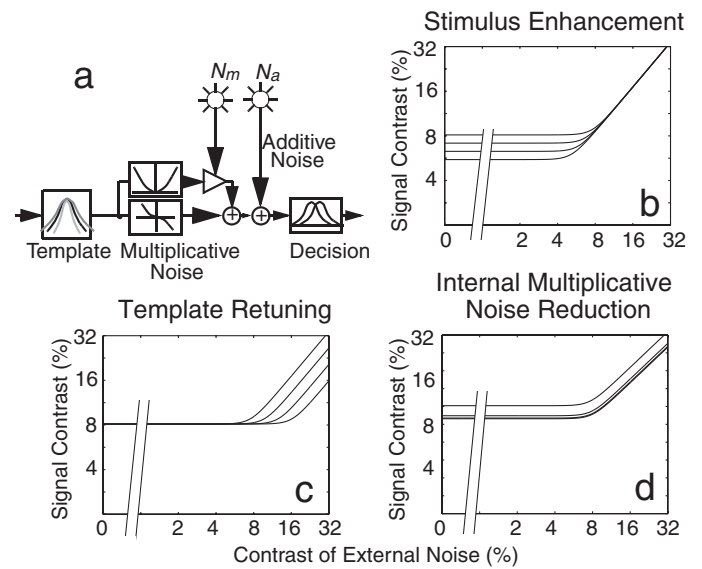


Figure 2. Perceptual template model (a) and performance signatures of the three mechanisms of perceptual learning (b, c, and d).

$$c_{\tau} = \frac{1}{\beta} \left[\frac{(1 + N_{mul}^2)N_{ext}^{2\gamma} + N_{add}^2}{(1/d'^2 - N_{mul}^2)} \right]^{2\gamma}. \quad (2)$$

A full specification of the parameters of a PTM requires measurements of TVC functions at a minimum of three threshold performance levels. In contrast to LAM, the PTM has been shown to provide an excellent account of threshold versus contrast functions at multiple performance levels and full psychometric functions across a wide range of external noise levels with a single set of parameters (Lu & Doshier, 1999).

Three mechanisms of perceptual learning can be distinguished within the PTM: *stimulus enhancement* reduces absolute thresholds by reducing internal additive noise; *perceptual template retuning* optimizes the perceptual template to exclude external noise or distractors; and *contrast-gain control reduction* decreases the impact of internal multiplicative noise. These three mechanisms exhibit signature performance patterns (Figure 2) when we compare TVC functions at several points during perceptual learning (Doshier & Lu, 1999). *Stimulus enhancement* increases the relative (vs. internal additive noise) gain of both the signal and the external noise in the stimulus and is associated with performance improvements only in low or zero external noise (Figure 2b). *Perceptual template retuning* improves the ability of the observer to exclude external noise and therefore is associated with performance improvements only in high external noise (Figure 2c). *Contrast-gain control reduction* increases system response to stimulus contrast and is associated with improvements throughout the full range of external noise (Figure 2d). In addition, we can distinguish various mechanism mixtures by measuring TVC functions at multiple performance levels (e.g., 70% and 80% correct).

The three mechanisms of perceptual learning in PTM provide a complete mathematical basis to accommodate all possible systematic patterns of performance improvements. An important theoretical question is whether one can empirically isolate each of the three mechanisms of perceptual learning within a task domain, and specify the circumstances under which these mechanisms operate.

In the domain of visual attention, pure cases of template retuning (Doshier & Lu, 2000a, 2000b; Lu & Doshier, 2000) and stimulus enhancement (Lu & Doshier, 1998; Lu & Doshier, 2000; Lu, Liu, & Doshier, 2000) have been documented separately and in different circumstances. And, the results from the PTM approach have already proved useful in recasting and reorganizing the existing attention literature (Doshier & Lu, 2000b).

In the PTM-based theoretical framework, very strong constraints are placed on the relative magnitude of perceptual learning across different performance levels for a given external noise condition (Doshier & Lu, 1999). On the other hand, performance improvements in the presence of high external noise are attributed to a mechanism of per-

ceptual template retuning, while improvements in the absence of external noise are attributed to a separate stimulus enhancement mechanism. In the LAM-based efficiency framework, performance improvements in the presence and absence of external noise are completely coupled for improved efficiency; additional improvements in the absence of external noise are accounted for by internal noise reduction. An empirical demonstration of larger performance improvements in high external noise than those in low external noise, a natural prediction of the PTM-based framework, would pose an empirical challenge to the LAM-based account of perceptual learning.

Dependence of the magnitude of perceptual improvements on external noise

The magnitude of perceptual learning may be highly dependent on the eccentricity of the stimulus presentation, the complexity of the task, and the presence or absence of mask/noise in the stimuli (Fine & Jacobs, 2002). For simple, in low-level tasks presented in fovea, a number of studies have documented the absence of or only small amount of perceptual learning in a clear field (Dorais & Sagi, 1997; Fiorentini & Berardi, 1981; Furmanski & Engel, 2000; Johnson & Leibowitz, 1979; Matthews, Liu, Geesaman, & Qian, 1999; Ramachandran & Braddick, 1973). Other studies using hyper-acuity (Bennett & Westheimer, 1991; McKee & Westheimer, 1978) or unfamiliar task situations (Matthews, Liu, & Qian, 2001; Vogels & Orban, 1985) did demonstrate perceptual learning in noiseless foveal displays. And whether perceptual learning improves absolute detection threshold in noiseless displays in fovea (Adini, Sagi, & Tsodyks, 2002; Mayer, 1983; Yu, Klein, & Levi, 2003) is still under debate. On the other hand, substantially more learning in fovea has been observed over a wide range of simple visual tasks using stimuli that contained external noise (Ball & Sekuler, 1982; Dorais & Sagi, 1997; Fine & Jacobs, 2000; Furmanski & Engel, 2000; Gold et al., 1999; Saarinen & Levi, 1995; Schoups et al., 1995).

Overview

In this study, we exploited the external noise dependency of the magnitude of perceptual improvements in fovea to test the theoretical constraint set by the LAM-based theory of perceptual learning. The aim of the study is to demonstrate that it is possible to observe a larger magnitude of learning in the presence of high external noise than that in the absence of external noise and therefore pose a challenge to the LAM-based theoretical framework. Although learning may of course occur in some circumstances in noiseless displays, the literature suggested that the magnitude of learning in noiseless condition might be limited, whereas learning in high noise circumstances might be more easily expressed.

In Experiment 1, we evaluated effects of perceptual learning in a simple foveal orientation identification task over a full range of systematically manipulated contrasts of

external noise. We compared the LAM- and PTM-based theoretical frameworks in their ability to account for the data. In Experiment 2, we evaluated whether further perceptual improvements can be obtained at a different viewing distance after the observers were trained at one particular viewing distance.

Methods

Apparatus

All stimuli were presented on a Nanao Technology FlexScan-6600 monitor with a P4 phosphor and a 120 frames/s refresh rate. The display was controlled by a 7500/100 Power Macintosh computer using a program based on PsychToolbox (Brainard, 1997; Pelli, 1997) in MATLAB (1998). A special circuit (Pelli & Zhang, 1991) combined two 8-bit output channels of the video card and divided the full luminance range of the monitor (1 to 53 cd/m^2) into 6144 distinct gray levels (12.6 bits). The display was gamma corrected using a psychophysical procedure (Lu & Sperling, 1999). All displays were viewed binocularly with natural pupil at a viewing distance of approximately 72 cm in Experiment 1 and 36 cm in Experiment 2 in a dimly lighted room.

Stimuli

The "signals" in the perceptual learning task were Gabor patterns tilted ± 8 deg clockwise or counter-clockwise from 45 deg:

$$I(x, y) = I_0 \left\{ \begin{array}{l} 1.0 + c \sin[2\pi f(x \cos(\pi(45 \pm 8) / 180) \\ + y \sin(\pi(45 \pm 8) / 180))] \exp(-\frac{x^2 + y^2}{2\sigma^2}) \end{array} \right\} \quad (3)$$

where background luminance $I_0 = 27 \text{ cd}/\text{m}^2$, Gabor center frequency $f = 1.34 \text{ c}/\text{deg}$, and Gabor spatial window $\sigma = 0.75 \text{ deg}$. The peak contrast c was set by the adaptive staircase procedures.

External noise images were generated using pixel contrasts drawn independently from identical Gaussian distributions. To increase the noise energy in the task-relevant spatial frequency channels, the external noise images were filtered with a pass-band from one octave below to one octave above the center frequency of the Gabors. The root mean square (RMS) contrast of the filtered images was set at 0, 0.021, 0.041, 0.083, 0.124, 0.165, 0.248, and 0.33. Whereas the maximum possible contrast in the display is 1.0, we limited the maximum SD of the external noise to 0.33 to conform to a Gaussian distribution.

Both the Gabor patterns and the noise frames were rendered on a 64×64 pixel grid ($3.0 \times 3.0 \text{ deg}$) and windowed by a 3.0-deg diameter disk to eliminate explicit cues for 45 deg in the display (Figure 3a and 3b).

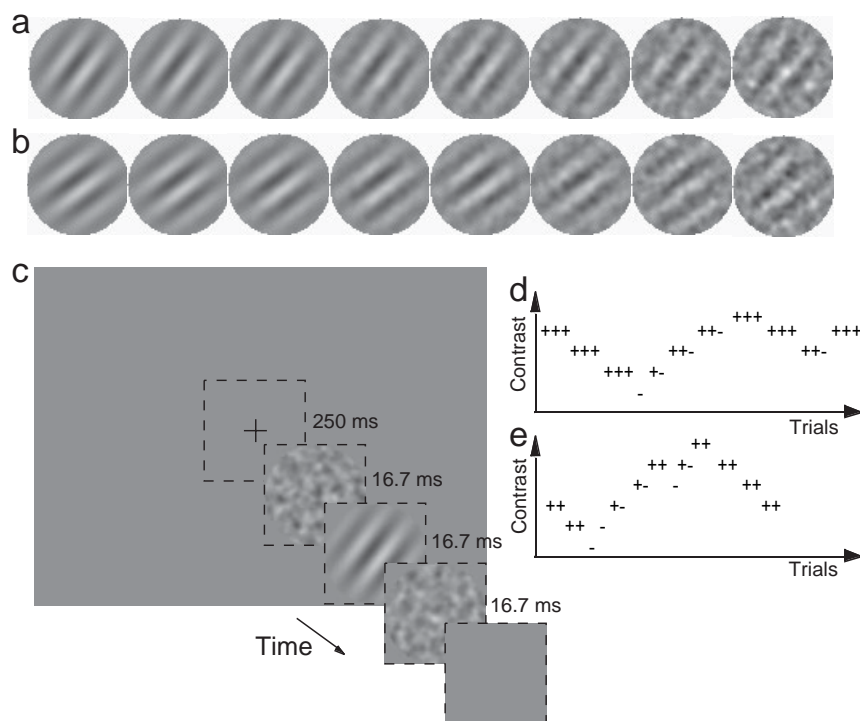


Figure 3. Stimuli and procedures. a. A high-contrast Gabor pattern embedded in external noise with increasing contrast levels. The Gabor is tilted 8 deg counter-clockwise from 45 deg. b. Same as a; the Gabor is tilted 8 deg clockwise from 45 deg. c. A display sequence. d. A sample 3/1 adaptive staircase segment. e. A sample 2/1 adaptive staircase segment.

Design and procedure

The display sequence of a typical trial is shown in Figure 3c. Following a key press, a fixation-cross appeared for 250 ms. A stimulus sequence was then presented in the center of the display: a frame of random external noise, a Gabor patch tilted either +8 or -8 deg from 45 deg, and another frame of random external noise, each lasting 16.7 ms. Both noise frames in each trial were independent samples from the same noise distribution. The noise is combined with the signal through temporal integration. The subject identified the orientation of the Gabor patch by pressing one of two keys. A brief beep followed each correct response.

Threshold contrasts at two performance criterion levels were estimated for the orientation identification task at each of the eight external noise levels using two interleaved staircase procedures (Levitt, 1971). One staircase procedure (Figure 3d) decreased signal contrast by 10% after three successive correct responses and increased signal contrast by 10% after every error (a three-down one-up or 3/1 staircase). It tracked a two-alternative forced-choice threshold at 79.3% correct (d' of 1.634) performance level. The other staircase procedure (Figure 3e) decreased signal contrast by 10% after two successive correct responses and increased signal contrast by 10% after every error (a two-down one-up or 2/1 staircase). It tracked a two-alternative forced-choice threshold at 70.7% correct (d' of 1.089) performance level.

All the experimental conditions and staircases were intermixed. There were 1,440 trials per session, consisting of 100 trials for each 3/1 staircase and 80 trials for each 2/1 staircase at each external noise level. Data were collected in 10 sessions on separate days. The staircases in every new session started from the contrasts in the end of the previous session.

To get better estimates of the thresholds, we pooled the data from the two staircases in each external noise condition and fitted psychometric functions to them using a maximum likelihood procedure (Hays, 1981). For each observer, there were 360 trials in each external noise condition in each training block. Five Weibull functions (Wichmann & Hill, 2001)

$$Pc(c) = \max - (\max - 0.5) 2^{-\left(\frac{c}{\alpha}\right)^\eta}, \quad (4)$$

with the same \max and η , but independent α 's, were fit to the five data sets in each external noise condition. Thresholds at $Pc = 70.7\%$ and $Pc = 79.3\%$ were computed from the psychometric functions in order to quantify threshold versus external noise contrast functions.

Observers

Four graduate students (aged 19 to 24 years), all with normal or corrected-to-normal vision and naive to the purposes of the experiment, participated in Experiment 1 with

informed consent. Three of these four observers participated in Experiment 2 immediately after they finished Experiment 1.

Modeling

Two mechanisms of perceptual learning based on the LAM

In the LAM-based theoretical framework, there are two mechanisms for perceptual improvements due to perceptual learning. The first mechanism, perceptual learning-induced efficiency improvement, is modeled by multiplying the perceptual efficiency E_τ in learning block t by a learning parameter $A_{E_\tau}(t)$. This learning parameter may in general depend on the performance level on which threshold is defined. If this dependency on criterion performance level occurs, this represents a failure of parameter consistency of the model. The second mechanism, perceptual learning-induced internal noise reduction, is modeled by multiplying the equivalent internal noise by $A_{eq}(t)$. From Equation 1, we have

$$c_{70.7\%}(N_{ext}, t) = \sqrt{\frac{A_{eq}^2(t)N_{eq}^2 + N_{ext}^2}{A_{E70.7\%}(t)E_{70.7\%}}} \quad (5a)$$

$$c_{79.3\%}(N_{ext}, t) = \sqrt{\frac{A_{eq}^2(t)N_{eq}^2 + N_{ext}^2}{A_{E79.3\%}(t)E_{79.3\%}}} \quad (5b)$$

The signature performance patterns of each of the two mechanisms and their mixture are shown in Figure 1. Without losing generality, we set $A_{eq} = 1.0$ and $A_{E70.7\%}(1) = A_{E79.3\%}(1) = 1.0$. This simply scales all learning in relation to the initial performance level. A full model of the data collected in Experiment 1, therefore, consists of N_{eq} , $E_{70.7\%}$, $E_{79.3\%}$, $A_{eq}(2, \dots, 5)$, $A_{E70.7\%}(2, \dots, 5)$, and $A_{E79.3\%}(2, \dots, 5)$, a total of 15 parameters.

Three mechanisms of perceptual learning based on the PTM

In the PTM-based theoretical framework, perceptual learning impacts performance in one or a combination of three different ways: (1) retuning the perceptual template differentially excludes external noise. This is modeled by multiplying the amount of external noise in learning block t by a learning parameter $A_f(t)$; (2) stimulus enhancement amplifies the stimulus (both the signal and the external noise). This is mathematically equivalent to reducing internal additive noise by $A_a(t)$ (Lu & Doshier, 1998); (3) changes in contrast-gain control properties result in a reduction of internal multiplicative noise by $A_m(t)$. Equation 2 can be modified to incorporate the learning parameters as follows:

$$c_\tau = \frac{1}{\beta} \left[\frac{(1 + (A_m(t)N_{mul})^2)(A_f(t)N_{ext})^{2\gamma} + (A_a(t)N_{add})^2}{(1/d'^2 - (A_m(t)N_{mul})^2)} \right]^{\frac{1}{2\gamma}}, \quad (6)$$

The signature performance patterns of each of the three mechanisms are shown in Figure 2. Again, without losing generality, we set $A_a(1)=1.0$, $A_a(1)=1.0$, and $A_a(1)=1.0$. A full model of the data collected in Experiment 1 therefore consists of N_a , N_m , β , γ , $A_a(2,\dots,5)$, $A_f(2,\dots,5)$, and $A_m(2,\dots,5)$, a total of 16 parameters.

Fitting procedures

Six forms of the LAM-based models were considered: (1) no perceptual learning (i.e., all learning parameters = 1.0), (2) changed equivalent internal noise, (3) improved efficiencies with separate magnitudes at different performance levels (independent $A_{E70.7\%}(t)$ and $A_{E79.3\%}(t)$), (4) improved efficiencies with same magnitudes at different performance levels ($A_{E70.7\%}(t) = A_{E79.3\%}(t)$), (5) a combination of (2) and (3), and (6) a combination of (2) and (4). In addition, eight forms of the PTM-based models were considered, ranging from no change of any learning parameter with increased training to changes of all the learning parameters with increased learning.

For each model form, the best-fitting model minimized the least square difference between the log of the measured threshold contrasts and the log of the model-predicted thresholds. The log is used to approximately equate the SE of the measured thresholds. The goodness of fit is gauged by the r^2 statistic

$$r^2 = 1.0 - \frac{\sum [\log(c_\tau^{theory}) - \log(c_\tau)]^2}{\sum [\log(c_\tau) - \text{mean}(\log(c_\tau))]^2}, \tag{7}$$

where \sum and $\text{mean}()$ were across all the practice and external noise conditions at both performance levels. Of the six LAM-based and eight PTM-based models, some are reduced models (proper subsets) of the others. *F*-tests for nested models were used to compare these models:

$$F(df_1, df_2) = \frac{(r_{full}^2 - r_{reduced}^2)/df_1}{(1 - r_{full}^2)/df_2}, \tag{8}$$

where $df_1 = k_{full} - k_{reduced}$, and $df_2 = N - k_{full}$. The k s are the number of parameters in each model, and N is the number of predicted data points. The minimal yet sufficient (i.e., statistically equivalent to the maximum) model was selected as the best-fitting model for the data, separately for the LAM-based and the PTM-based model lattices.

SDs were estimated for the parameters of the best-fitting LAM-based and PTM-based models using a re-sampling method (Maloney, 1990). Each of the 80 thresholds was assumed to have resulted from a normal distribution with its mean and SD equal to the estimated values from the experimental procedure. We “re-generated” 1,000 copies of theoretical datasets by drawing one sample from the 80 threshold distributions each time. We then fit the LAM-based and PTM-based models to each copy of the re-sampled datasets and calculated the SDs of the model parameters from the results of the fits.

Results

Experiment 1

TVC functions

In 10 sessions of practice, observers identified the orientation of a Gabor patch (a windowed sinusoidal grating) as tilted clockwise or counter-clockwise (± 8 deg) from 45 deg. The Gabor patches were tested in fovea in eight levels of external noise. Thresholds at two criterion performance levels ($P_c = 70.7\%$ and $P_c = 79.3\%$) were estimated in each external noise condition using adaptive staircase procedures (Figure 3d and 3e). This design yielded a total of 20 [10 sessions \times 2 criterion levels] TVC functions, each sampled at eight external noise levels. The average of these TVC functions across all the observers are shown in Figure 4, pooled over every two sessions.

Thresholds increased six-fold or more as external noise increased, from about 0.086 to 0.56 averaged across the training sessions. As expected, the less stringent performance criterion (70.7%) required lower thresholds than the more stringent performance criterion (79.3%). The thresh-

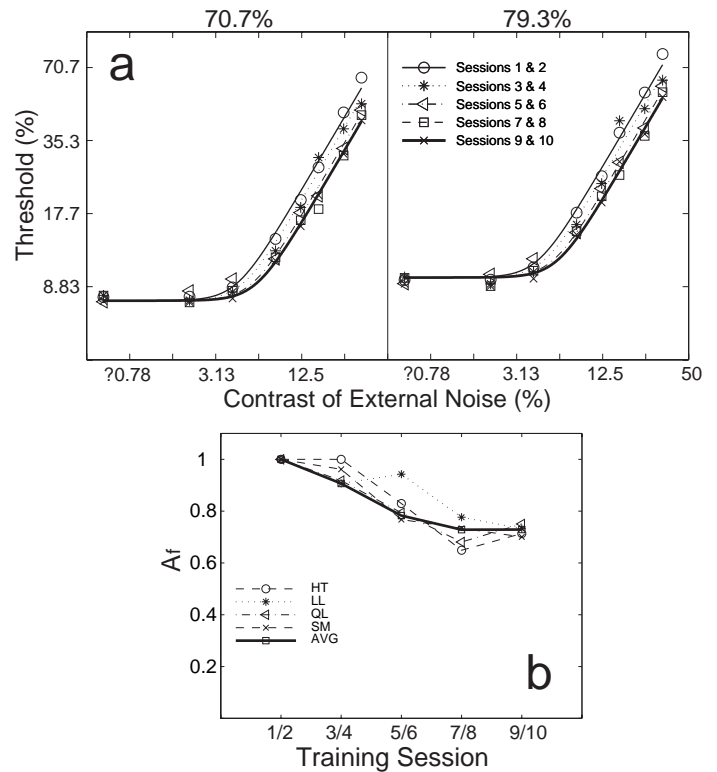


Figure 4. a. Threshold versus external noise contrast (TVC) functions at two performance-criterion levels (70.7% and 79.3% correct) over 10 training sessions in Experiment 1, averaged across the four observers. The smooth curves represent the best fit of the PTM model. The relative SEs of the thresholds are about 5%. b. A_f versus training session blocks for the four observers as well as the “average” observer AVG. For the average observer AVG, A_f reduced to 0.7289 after 10 sessions of practice.

old ratio between the two criterion levels is essentially constant across the eight noise levels and training sessions (mean= 1.24; SE = 0.024). Ratio constancy across external noise and practice levels indicates that practice did not alter contrast-gain control properties of the perceptual system (Doshier & Lu, 1999; Lu & Doshier, 1999).

No significant threshold reduction was observed in the noiseless condition on average over 10 days of practice. Contrast thresholds, averaged across observers and criterion levels, were about 0.087 in sessions 1 and 2 and 0.084 in sessions 9 and 10. On the other hand, substantial threshold reduction was observed in the high external noise conditions over 10 days of practice. Contrast thresholds, averaged across observers and criterion levels, reduced by about 33%, from 0.72 to 0.48 in the highest external noise condition. The magnitude of the improvement is representative of individual observers. In short, observers were specifically learning to exclude external noise. Independent of any particular model, the data provided an empirical demonstration of a pure, separable mechanism of perceptual learning that operates only in the presence of large amounts of external noise.

LAM-based modeling

In the LAM-based theoretical framework, more learning in high external noise than in low external noise requires a paradoxical account: a mixture mechanism of improved efficiency and increased damage to performance in internal noise. For the data shown in Figure 4a, the LAM-based model that assumes improved efficiencies with the same magnitude at different performance levels ($A_{E70.7\%}(t) = A_{E79.3\%}(t)$) and increased equivalent internal noise provided the best fit. With 11 parameters and $r^2 = 0.9915$, this model is statistically equivalent to the most saturated model ($F(4,65)=0.0031, p > .95$) and is superior to all the models with fewer learning mechanisms: (1) $F(4,69)=7.542, p < 5 \times 10^{-5}$, for a comparison with the model that assumes modifications of calculation efficiency but constant internal noise across training sessions; (2) $F(4, 69)=22.72, p < 10^{-11}$, for a comparison with the model that assumes internal noise changes but constant calculation efficiency across training sessions; and (3) $F(8,69)=12.12, p < 10^{-9}$, for a comparison with the model that assumes no learning at all. The parameters of the best-fitting model are shown in Table 1.

The predictions of the best-fitting LAM-based model are plotted in Figure 5a, along with the best-fitting A_E values in Figure 5b, and best-fitting A_{eq} values in Figure 5c.

According to the LAM-based model, perceptual learning improved efficiency by a factor of 1.95. It also increased internal noise by a factor of 1.4. Whereas learning-induced enhancement of efficiency results in equivalent performance improvements (threshold reduction) across all the external noise levels, an exactly compensatory increase of equivalent internal noise is necessary to account for the lack of perceptual learning in the low noise conditions. However, that perceptual learning increases equivalent in-

Parameter	Value	SE
N_{eq}	0.0417	0.0013
$E_{70.7\%}$	0.3484	0.0122
$E_{79.3\%}$	0.2261	0.0078
$A_{eq}(2)$	1.114	0.051
$A_{eq}(3)$	1.389	0.064
$A_{eq}(4)$	1.451	0.066
$A_{eq}(5)$	1.374	0.064
$A_E(2)$	1.234	0.057
$A_E(3)$	1.697	0.083
$A_E(4)$	1.979	0.096
$A_E(5)$	1.949	0.099

Table 1. Parameters of the LAM-based model.

ternal noise seems to be rather paradoxical, and the requirement that it does so by exactly the amount required to cancel the efficiency improvement appears to fail requirements of representativeness. Another paradoxical result from this modeling exercise is that the estimated calculation efficiency depends on performance criterion – in fact, lower efficiency for 79.3% correct than 70.7% correct. Both of these paradoxical results lead to questions about the internal coherence of the efficiency model account of perceptual learning.

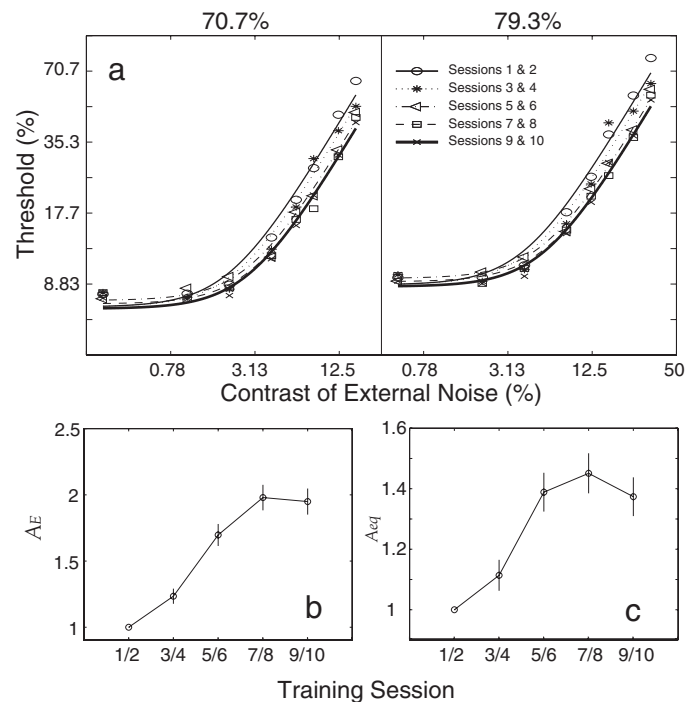


Figure 5. a. Threshold versus external noise contrast (TVC) functions at two performance-criterion levels (70.7% and 79.3% correct) over 10 training sessions in Experiment 1, averaged across the four observers. The smooth curves represent the best fit of the LAM model. A_E (b) and A_{eq} (c) as functions of training from the best-fitting LAM-based model.

Parameter	Value	SE
N_{add}	0.00115	0.00041
N_{mul}	0.037	0.081
β	0.579	0.011
γ	2.185	0.1348
$A_f(2)$	0.907	0.020
$A_f(3)$	0.783	0.018
$A_f(4)$	0.729	0.017
$A_f(5)$	0.729	0.016

Table 2. Parameters of the PTM-based model.

PTM-based modeling

In the PTM theoretical framework, learning only in the presence of relatively high external noise implies that perceptual learning retuned the perceptual template to selectively exclude external noise. The hypothesis was tested statistically. Perceptual template retuning was uniquely identified as the mechanism of perceptual learning underlying the observed performance improvements. With eight parameters and $r^2 = 0.9915$, this model is statistically equivalent to the fullest model that assumes all three perceptual learning mechanisms ($F(8,64) = 0.5582$, $p > .75$) and is superior to the model that assumes no perceptual learning at all ($F(4,72) = 12.63$, $p < 10^{-7}$). The parameters of the best-fitting model are shown in Table 2.

In summary, defining the impact of external noise to be 1.0 (100%) in (the average of) sessions 1 and 2, retuning of the perceptual template during perceptual learning reduced the impact of external noise to 0.907, 0.783, 0.729, and 0.729 in sessions 3 and 4, 5 and 6, 7 and 8, and 9 and 10 (Figure 4b). In other words, by sessions 7 and 8 and 9 and 10, the impact of the external noise was equivalent to 73% of the original impact of that same external noise in the beginning of the practice. The theoretical predictions of the best-fitting model are plotted in Figure 4a, along with the corresponding A_f values for the training sessions in Figure 4b.

Experiment 2

Experiment 2 was designed to evaluate the specificity of learning to spatial scale. Most studies that evaluate specificity of perceptual learning have used a three-stage design: initial evaluation of performance levels in several conditions, training or practice in one particular condition, and re-evaluation of performance levels in all the conditions. The specificity of perceptual learning is then evaluated by comparing performance levels before and after training.¹ Another design, frequently used in studies of cognitive learning but less frequently used in studies of perceptual learning, involves two stages: training or practice in one condition, and further training or practice in other conditions. In this design, the specificity of learning is evaluated

by measuring the amount of further learning in the conditions not included in the initial training. Depending on the learning rate and the number of trials involved in reliable performance measures, the two designs have different pros and cons (Pennington & Rehder, 1995). We chose the second design in this study because measurements of TVC functions at eight external noise and two performance levels involved relatively large numbers of trials (1,440/session).

In pilot studies, we observed perceptual learning at both 72- and 36-cm viewing distances. In the main experiment, three of the four observers were tested with exactly the same procedure used in Experiment 1, except at half the viewing distance. Over six training sessions, no further performance improvement was found at any level of external noise (Figure 6). Statistical testing failed to identify further learning ($p > .25$). This suggests a complete transfer of perceptual learning of the orientation identification task at fovea to a viewing distance at half of the original. If transfer had not been complete, practice at the new scale would have produced new learning, which was not observed. In other words, perceptual learning of this task is scale invariant in the range tested (1 to 2). The best-fitting model has four parameters (N_{add} , N_{mul} , β , γ) with $r^2 = 0.9959$.

Discussion and conclusions

The observed lack of perceptual learning in the noiseless condition and substantial learning in higher external noise conditions in foveal orientation identification is consistent with the results of a number of studies in the literature (Ball & Sekuler, 1982; Dorais & Sagi, 1997; Fine & Jacobs, 2000; Fiorentini & Berardi, 1981; Furmanski & Engel, 2000; Gold et al., 1999; Johnson & Lebowitz, 1979; Matthews et al., 1999; Ramachandran & Braddick, 1973; Saarinen & Levi, 1995; Schoups et al., 1995). On the other hand, several other studies have demonstrated perceptual learning in fovea in noiseless displays (Bennett & Westheimer, 1991; Matthews et al., 2001; Mayer, 1983; McKee & Westheimer, 1978; Vogels & Orban, 1985; Yu et al., 2003). The exact nature of external noise dependence of foveal perceptual learning in this and other tasks requires further systematic investigation.

The observed pattern of perceptual learning – its dependence on the amount of external noise added to the signal stimulus – poses major challenges to the LAM-based accounts of perceptual learning (Gold et al., 1999). The performance improvements in high external noise conditions required improved calculation efficiency in the LAM-based model, which predicts equivalent performance improvements (threshold reduction) across all the external noise levels. However, because no learning or less learning was observed in low external noise conditions, paradoxical compensatory increases of the equivalent internal noise were necessary to account for the lack of perceptual learning in the low noise conditions. This plus the lack of a

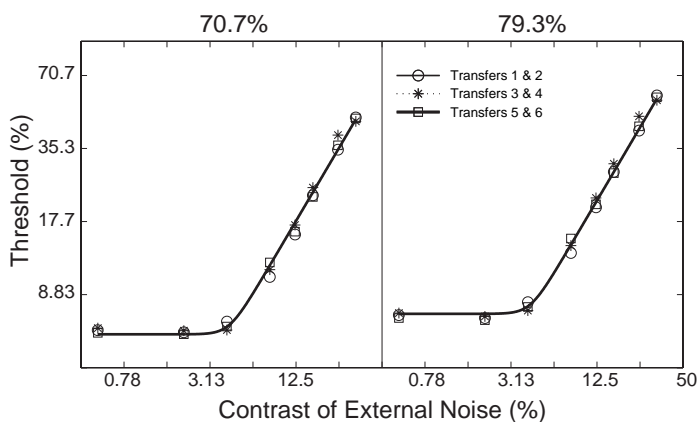


Figure 6. Threshold versus external noise contrast (TVC) functions at two performance criterion levels (70.7% and 79.3% correct) over six training sessions in Experiment 2, averaged across the three observers. The smooth curves are the best fits of the PTM model.

principled account of the calculation efficiency at different performance-criterion levels render the LAM-based theoretical framework both inconsistent and less parsimonious.

In contrast, the PTM model provides a coherent account of data in both attention and perceptual learning across multiple performance levels and task situations (Lu & Doshier, 2002b; Tjan et al., 2002). We conclude, based on the PTM framework, that perceptual learning in this task involved learning how to better exclude external noise. The PTM framework specifies two separate mechanisms of improved performance in noiseless and high noise conditions. The empirical result alone demonstrates the possibility of observing one mechanism – external noise exclusion – in the absence of the other.

The nature of adult plasticity underlying these changes in performance with perceptual learning in visual tasks is still under debate. Topographical reorganization of cortical maps reflecting neuronal recruitment as a result of perceptual learning has been documented in primary somatosensory cortex (Elbert, Pantev, Wienbruch, Rockstroh, & Taub, 1995; Recanzone, Merzenich, & Schreiner, 1992) and primary auditory cortex (Bakin & Weinberger, 1990; Durup & Fessard, 1935; Recanzone, Schreiner, & Merzenich, 1993; Weinberger, Ashe, Metherate, McKenna, Diamond, & Bakin, 1990). Cortical changes in primary visual cortex associated with perceptual learning have shown a lack of topographical map reorganization (Crist, Li, & Gilbert, 2001; Ghose, Yang, & Maunsell, 2002; Schoups, Vogels, Qian, & Orban, 2001). While one study (Schoups et al., 2001) found some modest changes of orientation tuning in V1 that accounted for a small fraction of the behavioral improvement, others (Crist et al., 2001; Ghose et al., 2002) failed to find any pronounced changes in neural responsiveness associated with behavioral improvements with tasks suited for early visual cortical areas. A recent computational model of perceptual learning (Petrov, Doshier, &

Lu, 2003) accounted for a very complex behavioral data set in a non-stationary environment through incremental channel re-weighting without altering early stages of visual processing, lending an existence proof of re-weighting of early visual channels as a plausible mechanism of perceptual learning (Doshier & Lu, 1998; Ghose et al., 2002; Mollon & Danilova, 1996). At the overall system level, a mechanism of perceptual template retuning reflects channel re-weighting, which can have larger consequences for external noise exclusion in high noise conditions.

In Experiment 2, we observed no further learning of the foveal orientation identification task at a viewing distance half of the original. The result suggests a complete transfer of perceptual learning to the new viewing distance. Manipulating viewing distance while keeping the visual display constant simultaneously changes the spatial frequency and the size of the stimuli on the retina but preserves object frequency (Parish & Sperling, 1991). It corresponds to changes of receptive field properties in V1 at different spatial frequency scales. Transfer of perceptual learning from one viewing distance to another therefore implies scale invariance in the learning mechanism and a form of learning that may generalize within a hyper-column of visual system. It might also suggest that equivalent computations at multiple resolution (or scales) of the visual pyramid may share learning at one particular scale of resolution. Because the range of viewing distance change was rather limited in this experiment (from 2 to 1), we can't draw any general conclusions about scale invariance of perceptual learning in fovea. However, the results are highly suggestive and will certainly deserve further investigation.

Doshier and Lu (1998, 1999) concluded that based on perceptual learning of orientation identification in visual periphery, the mechanism of perceptual learning consisted of a mixture of stimulus enhancement and template retuning. In this study, we found that a single template retuning accounted for performance improvements in foveal orientation identification. There are three primary differences between the two sets of experiments: (1) orientation identification was tested in fovea in the current study, but in the periphery in Doshier and Lu (1998, 1999), (2) there was a simultaneous central letter identification task at fixation in Doshier and Lu (1998, 1999), and (3) observers identified orientations at ± 15 deg from vertical in Doshier and Lu (1998, 1999) but ± 8 deg from 45 deg in the current study. Each of these factors probably partially contributes to the different empirical results, although the relative importance of the contributions remains to be specified. In general, they suggest that the mechanism of perceptual learning for any particular task may depend on the exact nature of the neural computation and/or visual pathway involved in performing that task.

The current study provides the first empirical demonstration of a pure, that is, isolated, *perceptual template retuning* mechanism of perceptual learning in a psychophysical study. The results are important for theories of perceptual learning because they behaviorally demonstrate the exist-

tence of an isolable mechanism. Much as the spectroscopic methods of atomic physics enabled physicists to unravel the structure of atoms, applications of the external noise method will enable us to discover the different mechanisms of perceptual learning.

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Footnotes

¹In certain designs, because of the inherent symmetry between the conditions, the first stage can be omitted.

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