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Mechanisms of perceptual learning

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Abstract

Systematic measurements of perceptual learning were performed in the presence of external or stimulus noise. In the new external noise method (Dosher, B, & Lu, Z.-L. (1997). *Investigative Ophthalmology and Visual Science*, *38*, S687; Lu, Z.-L., & Dosher, B. (1998). *Vision Research*, *38*, 1183–1198), increasing amounts of external noise (white Gaussian random noise) is added to the visual stimulus in order to identify mechanisms of perceptual learning. Performance improved (threshold contrast was reduced) over days of practice on a peripheral orientation discrimination task—labelling Gabor patches as tilted slightly to the right or left. Practice improvements were largely specific to the trained quadrant of the display. Performance improved at all levels of external noise. The external noise method and perceptual template model (PTM) of the observer identifies the mechanism(s) of performance improvements as due to *stimulus enhancement*, *external noise exclusion*, or *internal noise suppression*. The external noise method was further extended by measuring thresholds at two threshold performance levels, allowing identification of mixtures in the PTM model. Perceptual learning over 8–10 days improved the filtering or exclusion of external noise by a factor of two or more, and improved suppression of additive internal noise—equivalent to stimulus enhancement—by 50% or more. Coupled improvements in external noise exclusion and stimulus enhancement in the PTM model may reflect channel weighting. Perceptual learning may not reflect neural plasticity at the level of basic visual channels, nor cognitive adjustments of strategy, but rather plasticity at an intermediate level of weighting inputs to decision.

Keywords: Perceptual stimulus; Signal enhancement; External noise exclusion; Internal noise suppression; Additive internal noise; Multiplicative internal noise; Equivalent internal noise; Perceptual template model; Concurrent paradigm

1. Mechanisms of perceptual learning

Performance on perceptual tasks often improves with practice or training, but the mechanisms which underlie perceptual learning are still under debate. Training improves performance over a wide range of perceptual tasks in the visual domain, and some of what is learned is specific to stimulus factors such as retinal location, spatial frequency, or orientation. Perceptual learning that is highly specific to retinal location and stimulus has been claimed to reflect neural plasticity in basic visual processing mechanisms. In this paper, we report a new set of empirical observations of perceptual learning under systematic variations of environmental noise. Theoretically, this allows a systems analysis of the mechanisms of improvements in performance with practice. The results are consistent with perceptual learning that reflects plasticity in the weighting of inputs from basic visual mechanisms to decision.

Perceptual learning is quantified within a perceptual template model (PTM) which has recently been used to identify the mechanisms of voluntary perceptual attention to a spatial location (Dosher & Lu, 1997; Lu & Dosher, 1998a). This approach considers stimulus enhancement, external noise exclusion, and internal (multiplicative) noise reduction as possible mechanisms of improvement in performance of perceptual tasks. An external noise paradigm calibrates processing inefficiencies in the visual system in terms of equivalent internal noise. Using the external noise manipulation and a training paradigm, the nature of perceptual learning may be operationally characterized. This paper applies

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the external noise paradigm and PTM model to an orientation discrimination (or identification) task. Perceptual learning in this task is shown to reflect improvement in both stimulus enhancement and external noise exclusion. The variants of PTM model and the relationship of the empirical signatures to processing in visual system are also considered.

1.1. Learning in perceptual tasks

Improvements in task performance with training or with practice occur in a range of perceptual tasks. As early as 1973 (see Gibson (1969) for a review of earlier work), orientation-specific learning effects in adults were reported for the time to perceive patterns in random dot stereograms (Ramachandran & Braddick, 1973). In the succeeding years, perceptual learning effects have been reported in detection and discrimination of visual gratings (DeValois, 1977; Fiorentini & Berardi, 1980, 1981; Mayer, 1983), stimulus orientation judgments (Vogels & Orban, 1985; Shiu & Pashler, 1992), motion direction discrimination (Ball & Sekuler, 1982, 1987; Ball, Sekuler & Machamer 1983), texture discrimination (Karni & Sagi, 1991, 1993), stereoacuity (Fendick & Westheimer, 1983), and hyperacuity and vernier tasks (McKee & Westheimer, 1978; Bennett & Westheimer, 1991; Fahle & Edelman, 1993; Kumar & Glaser, 1993; Beard, Levi & Reich, 1995; Saarinen & Levi, 1995).

Improvement in performance is said to reflect perceptual learning, as opposed to cognitive learning, strategy selection, or motor learning, when the improvement exhibits specificity to either a retinal location or to a basic stimulus dimension such as spatial frequency, orientation, or scale. For example, improvement in a texture discrimination task was found to be specific to the orientation of the background texture elements and to retinal location (Karni & Sagi, 1991, 1993); improvement on motion direction discrimination for random dot fields was specific to the training direction (Ball & Sekuler, 1982); and improvements in discrimination of compound gratings were reported to be specific to both orientation and spatial frequency (Fiorentini & Berardi, 1980). Thus, failures of transfer to different retinal locations and to different stimuli are critical to conclusions about the nature and locus of perceptual learning. (The conditions of transfer specificity have, however, been challenged (Ahissar & Hochstein, 1997; Liu & Vaina, 1998).) There is a strong case for the perceptual nature of learning in many of these tasks. However, it is far more difficult to unambiguously identify the mechanism of the improvements. Transferability addresses generalizability and not the mechanisms themselves.

One recent attempt to further specify the nature of perceptual learning (Saarinen & Levi, 1995) performed a series of masking studies to evaluate whether improvements in vernier acuity reflect "'fine tuning' of the visual mechanisms" in orientation-tuned visual channels. They measured the dependence of mask effectiveness on mask orientation and concluded that orientation-specific channels may have been tuned during the course of practice on a vernier task (but see Beard and Ahumada (1997) for an alternative conclusion). This paper takes a different approach. An external noise paradigm is used to identify the mechanisms of perceptual learning. (For a preliminary report, see Dosher & Lu, 1998.)

1.2. The perceptual template model

A noisy perceptual template model (PTM) combined with the manipulation of external noise in the stimulus characterizes improvements in performance with perceptual learning. In a prior application of the PTM to a spatial attention task (Dosher & Lu, 1997; Lu & Dosher, 1998a), distinctive performance signatures were derived for improvements associated with stimulus enhancement, external noise exclusion, and internal noise reduction. In this section we outline the perceptual template model. Some readers may choose to proceed directly to the following section, which details the signature patterns associated with different mechanisms of improvement with practice.

The PTM model describes the input–output relationships of the perceptual and decision process for the observer as a system. Perceptual task performance by human observers near threshold reflects various processing inefficiencies, which may include coarse coding of stimulus properties, loss during information transmission, neural randomness, etc. as well as stimulus sampling limits such as photon noise, receptor noise and sampling noise. These processing inefficiencies and limits can be characterized in terms of the equivalent internal noise—the amount of random internal noise necessary to reduce performance to the observed level (Barlow, 1956; Nagaraja, 1964; Pelli, 1981; Ahumada & Watson, 1985). Equivalent internal noise is estimated by comparison to the effects of external noise in the stimulus.

To illustrate the impact of external noise on performance, a signal—in this case an oriented Gabor patch—is shown with several levels of external noise in Fig. 1a, b. Addition of external noise to signal has a characteristic impact on task performance. Task performance is measured by the signal contrast necessary to reach a threshold or criterion level of accuracy in a detection, discrimination or identification task. Graphs of threshold contrast as a function of external noise level (Fig. 1c), often called threshold versus contrast (TVC) functions, are generally flat in the region of low external noise, and then increase in regions of higher

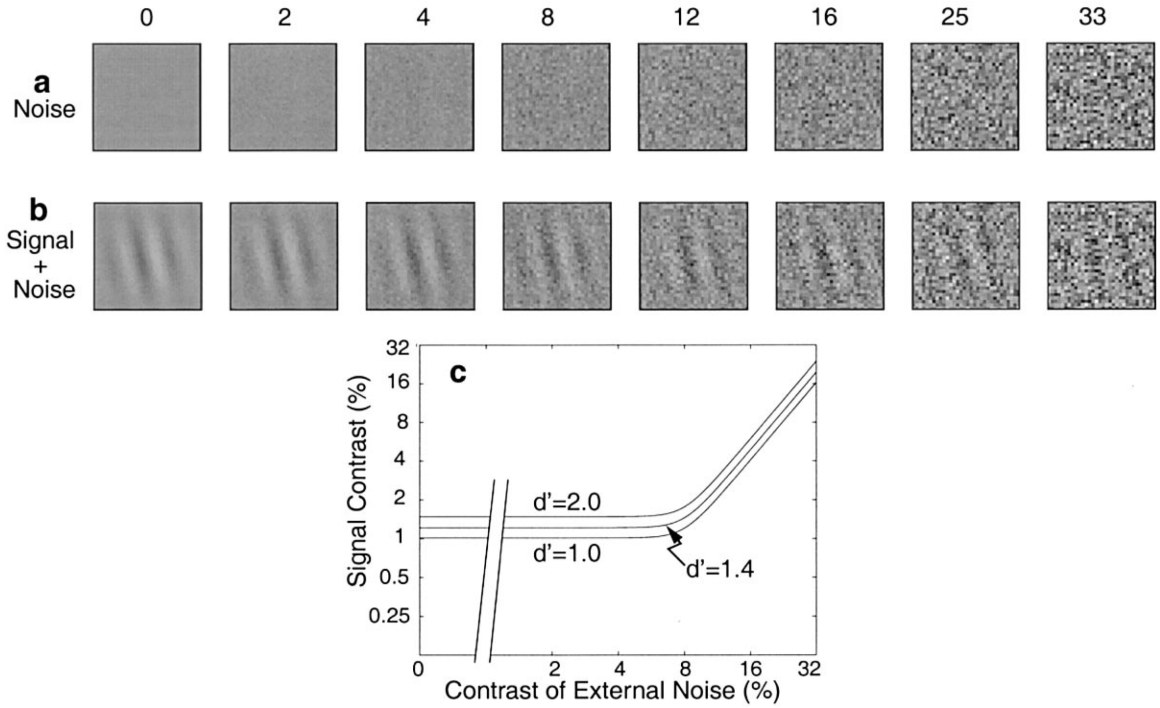

Fig. 1. Signal detection and discrimination are limited by external environmental or image noise. (a) Examples of external noise of increasing contrast levels. (b) Oriented Gabor signals embedded in external noise. (c) A typical performance function showing increases in signal contrast required to achieve threshold in increasing levels of external noise. Performance is limited by internal noise or processing limits at low levels of external noise, and by image noise at high levels of external noise. The smooth functions are hypothetical performance functions under the perceptual template model at three criterion levels of d'.

external noise. In the flat region of lower external noise, performance is limited not by the external noise, but by internal noise. In the region of higher external noise, external noise (and the consequent multiplicative internal noise) limits performance. The upper limb of the function reveals the impact of external noise while the lower limb of the function reveals the equivalent internal noise.

Functions of precisely this kind arise from a perceptual template model (PTM) illustrated in Fig. 2. The PTM characterizes human performance in perceptual tasks in terms of a signal processing filter or template, an optional transducer nonlinearity, an internal additive noise source, and an internal multiplicative noise source. The stimulus consists of a signal plus external noise. The internal additive noise source is independent of the contrast of the stimulus; the internal multiplicative noise source increases directly with the contrast of the stimulus (signal plus external noise). All noise sources are assumed to be independent. Several variants of this basic model with alternative arrangements of noise sources are considered in detail in Section 5 and Appendix A. The conclusions are consistent over broad classes of models.

The basic equations of the PTM model (see Lu and Dosher (1998a), Lu & Dosher (1999) for a development) are summarized briefly here. In the PTM model, accuracy of perceptual task performance is indexed by d', in which signal strength, S, is compared with the standard deviation of the total noise (external and internal), σ_N, or $d' = S/\sigma_N$. The signal plus external noise is processed by a task-relevant template or filter. The strength of response of the perceptual template is βc, where c is the contrast of the signal, and β is the gain on a signal-valued stimulus processed through the template or filter[1]. Multiplicative noise is proportional to the signal plus external noise contrast.

System output is not always a linear function of the input, reflecting either contrast gain control nonlinearities or nonlinear transduction. If the slope of the rising,

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[1] The contrast of a signal is a function of space and time: $S(x, y, t) = cS_0(x, y, t)$ rescaled such that $\iiint S_0^2(x, y, t)\mathrm{d}x\mathrm{d}y\mathrm{d}t = 1.0$. The contrast of the external noise is $N(x, y, t) = N_{\mathrm{ext}}G(x, y, t)$, where the value of $G(x, y, t)$ is drawn from a Gaussian distribution with mean 0 and standard deviation 1. Given a template function $T(x, y, t)$, matching the template to the signal yields output $T_S = \iiint T(x, y, t)S(x, y, t)\mathrm{d}x\mathrm{d}y\mathrm{d}t = c\iiint T(x, y, t)S_0(x, y, t)\mathrm{d}x\mathrm{d}y\mathrm{d}t$, which for a chosen template and signal is cT_{S_0}, where T_{S_0} is a constant. Correspondingly, matching the template to the external noise yields output $T_N = \iiint T(x, y, t)N(x, y, t)\mathrm{d}x\mathrm{d}y\mathrm{d}t = N_{\mathrm{ext}}\iiint T(x, y, t)G(x, y, t)\mathrm{d}x\mathrm{d}y\mathrm{d}t$. $T_G = \iiint T(x, y, t)G(x, y, t)\mathrm{d}x\mathrm{d}y\mathrm{d}t$ is a Gaussian random variable with mean 0 and standard deviation σ_{T_G}. We can rescale so that $T_N = N_{\mathrm{ext}}G(0, 1)$ and $T_S = \beta c$, where $\beta = T_{S_0}/\sigma_{T_G}$. That is, β is directly proportional to the correlation of the template and the signal.

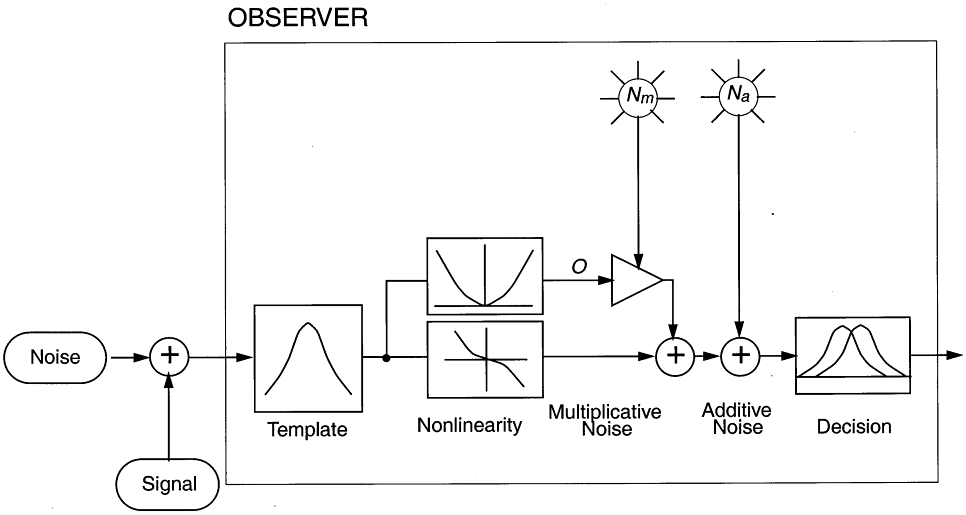

Fig. 2. A schematic diagram of the perceptual template model. Signal plus noise in the stimulus is processed through a task-relevant perceptual template, followed by nonlinear transducer functions applied to the signal and to the control of multiplicative noise, multiplicative and additive internal noises and a decision process. The internal noise sources quantify processing inefficiencies in the observer.

high external noise limb of the performance functions have slopes significantly different from one, e.g. (Dosher & Lu, 1997; Lu & Dosher, 1998a), or if performance at different criterion levels does not scale directly with the ratio of d's (Lu & Dosher, 1999), nonlinearities must be considered. The precise form of nonlinearities in visual system is still being actively investigated in studies of pattern masking and contrast gain control (Legge & Foley, 1980; Wilson, 1980; Foley & Legge, 1981; Foley, 1994). Nonlinearities may occur in both the signal and the multiplicative noise paths of the PTM model (Fig. 2). Following the approach in the pattern masking literature, the nonlinearities are modeled as power functions. The nonlinearity $\|\cdot\|^{\gamma_1}$ applies in the signal path and nonlinearity $\|\cdot\|^{\gamma_2}$ applies in the multiplicative noise path.

The signal strength including nonlinearity is $(\beta c)^{\gamma_1}$. And, since all noise sources are assumed to be independent, then $\sigma_N^2 = \sigma_{\text{ext}}^2 + \sigma_{\text{mul}}^2 + \sigma_{\text{add}}^2$, or $N_{\text{ext}}^{2\gamma_1} + N_m^2(\beta^{2\gamma_2}c^{2\gamma_2} + N_{\text{ext}}^{2\gamma_2}) + N_a^2$. The N^2.s refer to the variances of the external, internal additive and internal multiplicative noise sources which limit performance accuracy.

Overall performance is described by Eq. (1):

$$d' = \frac{(\beta c)^{\gamma_1}}{\sqrt{N_{\text{ext}}^{2\gamma_1} + N_m^2(\beta^{2\gamma_2}c^{2\gamma_2} + N_{\text{ext}}^{2\gamma_2}) + N_a^2}}. \quad (1)$$

For the case of $\gamma = \gamma_1 = \gamma_2$, a simple solution for the log form of the TVC (Fig. 1c) is derived by choosing a threshold d' and solving for a threshold level of contrast, c_τ.[2] In log form (Eq. (2)),

$$\log(c_\tau) = \frac{1}{2\gamma}\log((1+N_m^2)N_{\text{ext}}^{2\gamma} + N_a^2) - \frac{1}{2\gamma}\log(1/d'^2 - N_m^2) - \log(\beta). \quad (2)$$

1.3. *Mechanisms of perceptual task improvement*

The signature patterns of perceptual learning in an external noise paradigm for three pure mechanisms of improvement are shown in Fig. 3[3]. These signatures, developed qualitatively below, illustrate forms of improvement in performance which might result from attention or from perceptual learning.

One possible mechanism of improvement given either attention or perceptual learning involves *stimulus enhancement*—turning up the gain on the output of the signal-relevant perceptual template (see Fig. 3a, b). Stimulus enhancement is generally indistinguishable from reductions in internal additive noise (Lu & Dosher, 1998a) and this is the model form used in the current development. The signature pattern is improvement in the lower noise limb of the TVC functions: Turning up the gain on the stimulus (signal plus external noise), or equivalently reducing internal additive noise, improves performance at low external noise levels when internal noise is the limiting process. It cannot

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[2] Cross products in the form $(\beta^2c^2 + N_{\text{ext}}^2)^{\gamma_2}$ are eliminated in order to yield direct solutions. Model fits were also performed on the full cross product form by methods of iterative solution. The results of those model fits were equivalent in pattern and the cross product terms were small. The model was also evaluated for independent γ_1 and γ_2 by iterative solution; the $\gamma = \gamma_1 = \gamma_2$ solutions gave a good account of the current data.

[3] These pure mechanisms are empirically achievable in the current form of PTM model, but may not be in other forms (see Appendix A). Nonetheless, these pure forms serve as a descriptive basis set.

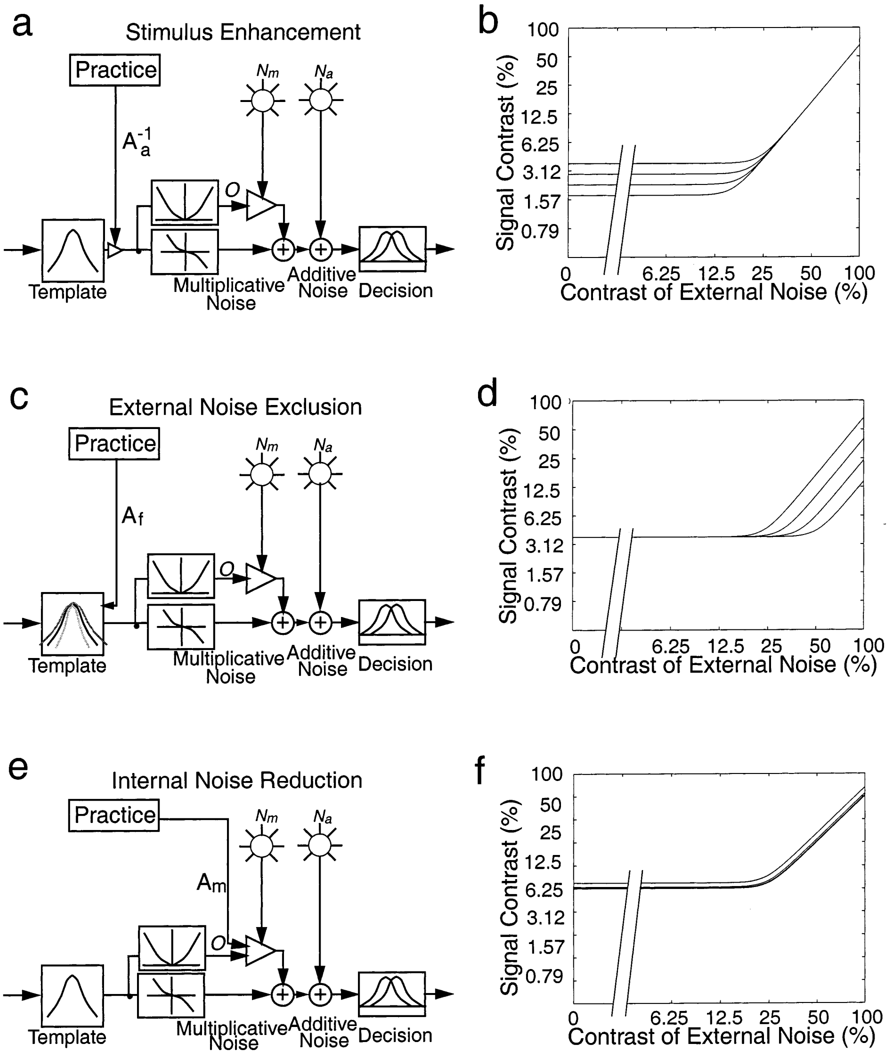

Fig. 3. Three mechanisms of perceptual learning and the corresponding performance signatures. (a) Practice that turns up the gain on the stimulus, corresponding to stimulus enhancement. (b) Stimulus enhancement is associated with improvements in performance in the lower noise limb of the contrast threshold functions. (c) Practice that affects the amount of external noise processed through the perceptual template by narrowing the filter tuning, corresponding to external noise exclusion. (d) External noise exclusion improves performance only in the high noise limb of the contrast threshold functions. (e) Practice that reduces the gain on multiplicative internal noise, or internal multiplicative noise reduction. (f) Internal (multiplicative) noise reduction improves performance somewhat over both limbs of the contrast threshold functions.

improve performance at high levels of external noise where external noise is the limiting factor, because increasing the gain on the signal increases the gain on external noise exactly to the same degree.

Another mechanism of improvement given either attention or perceptual learning involves *external noise exclusion*—eliminating some of the external noise by tuning the perceptual template or filter more narrowly around the signal-valued stimulus. This mechanism produces a signature pattern of improvement in the higher external noise limb of the TVC functions (see Fig. 3c, d). Narrowing the perceptual filter or template around the signal serves to exclude external noise in the stimulus, primarily affecting performance in the high external noise conditions where external noise is the limiting factor.

Finally, another possible mechanism of improvement in performance is *internal noise suppression*—the reduction of (multiplicative) internal noise. In this case, the signature pattern in performance involves improvement in both the low and high external noise regions (see Fig. 3e, f). The extent of improvement increases slightly at high external noise, since multiplicative noise is determined in part by the level of external noise.

Assuming that all three mechanisms of improvement may be operative (and that $\gamma = \gamma_1 = \gamma_2$), the PTM equation, in log form, is Eq. (3):

$$\log(c_\tau) = \frac{1}{2\gamma}\log((1 + A_m^2(k)N_m^2)A_f^{2\gamma}(k)N_{\text{ext}}^{2\gamma} + A_a^2(k)N_a^2) - \frac{1}{2\gamma}\log(1/d'^2 - A_m^2(k)N_m^2) - \log(\beta). \quad (3)$$

This equation is identical to the earlier equation except for the inclusion of multipliers $A \cdot (k)$, generally proportions less than one. The index k is a condition index. $A_a(k)$ are multipliers on internal additive noise associated with stimulus enhancement (internal additive noise reduction). The $A_f(k)$ are multipliers on the output of the perceptual filter applied to external noise, reflecting the width of the perceptual filter around the signal valued stimulus, corresponding to external noise exclusion. The $A_m(k)$ are multipliers on internal multiplicative noise associated with (multiplicative) internal noise reduction.

The PTM model and an attention plus external noise paradigm were applied to an orientation identification task in which the subject decided whether peripheral Gabor patches were tilted top to the right or top to the left (± 12°) (Dosher & Lu, 1997; Lu & Dosher, 1998a). Instructions to attend to a stimulus on either the right or left of fixation improved performance on the attended relative to the unattended side only in low external noise conditions; attention had no effect in the high external noise conditions. This is the signature for a stimulus enhancement mechanism, or, equivalently, the reduction of additive noise. Thus, this case of voluntary attention to a peripheral spatial location in a two-location orientation discrimination task is a demonstration of a *single* mechanism signature, wherein only A_a varies with condition. In contrast, precuing of report location affects performance only in high external noise conditions of a four-location, four-alternative identification task (Dosher & Lu, 1999), the signature for external noise exclusion. This provides a demonstration of the single mechanism case wherein only A_f varies with condition.

Mixtures of more than one mechanism may underlie improvement in performance associated with either attention or perceptual learning in some tasks. An examination of Fig. 3 suggests that a mixture of stimulus enhancement and external noise exclusion signatures might look very similar to the signature for multiplicative internal noise suppression. For situations with nonlinearities affecting the slope of the TVC function ($\gamma_1 \neq \gamma_2$) mixtures may be discriminated relatively directly in the model (Lu & Dosher, 1998a). In other cases, additional data may be required. The issue of identifying mixtures is considered in detail after the presentation of Experiment 1.

1.4. Summary

The PTM model provides an analysis at a whole system level of the observer in a particular task. The external noise paradigm allows the identification of improvements in performance with perceptual learning, with one or more of the system mechanisms, stimulus enhancement, external noise exclusion, and internal (multiplicative) noise reduction. Linking hypotheses are required to relate the whole system analysis to the operation of basic mechanisms in visual processing (Graham, 1989). Patterns of performance of our observers in the presence of external noise are related in Section 5.4 to the processing of analysers or filters in early visual system.

2. Experiment 1

The goal of this research was to discover the mechanisms underlying the improvement in performance in a perceptual learning task using the external noise paradigm. The pattern of improvement at both low and high external noise levels can be used to identify the mechanisms of improvement with practice. For this initial study, we chose a paradigm which is similar to the perceptual learning studies of Karni and Sagi (1991, 1993), who found that perceptual learning was specific to retinal location.

As in prior studies, the observer is asked to perform two tasks: In the central task, fixation is maintained on a central point and the observer discriminates an S from a 5 in a rapidly presented string of small characters (see Fig. 4). Simultaneously, the perceptual task is presented in the visual periphery. The perceptual task was an orientation discrimination task, essentially requiring identification of which of two stimuli was presented. A Gabor patch was tilted either ± 12° from vertical, and the observer reported whether the patch tilted top to the right or top to the left. The patch was combined with external noise, and the contrast required for threshold performance was measured. The task was similar to, but easier than, that of Lu and Dosher (1998a)[4].

The mechanism(s) of perceptual learning at the whole system level may be associated with stimulus enhancement, external noise exclusion, or internal noise suppression, or some combination. Certain earlier claims about neural plasticity (Karni & Sagi, 1991, 1993) have focused on lack of transfer to other retinal locations. Therefore, transfer to untrained locations in the periphery is also examined.

2.1. Method

2.1.1. Stimulus and display

The signals in the perceptual learning task were Gabor patterns tilted either $\theta°$ to the right or left of vertical:

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[4] The current task was easier than the task in Lu and Dosher in that it presented a larger pixel grid with more sidebars per Gabor than the previous stimulus. The overall luminance levels at threshold were correspondingly lower.

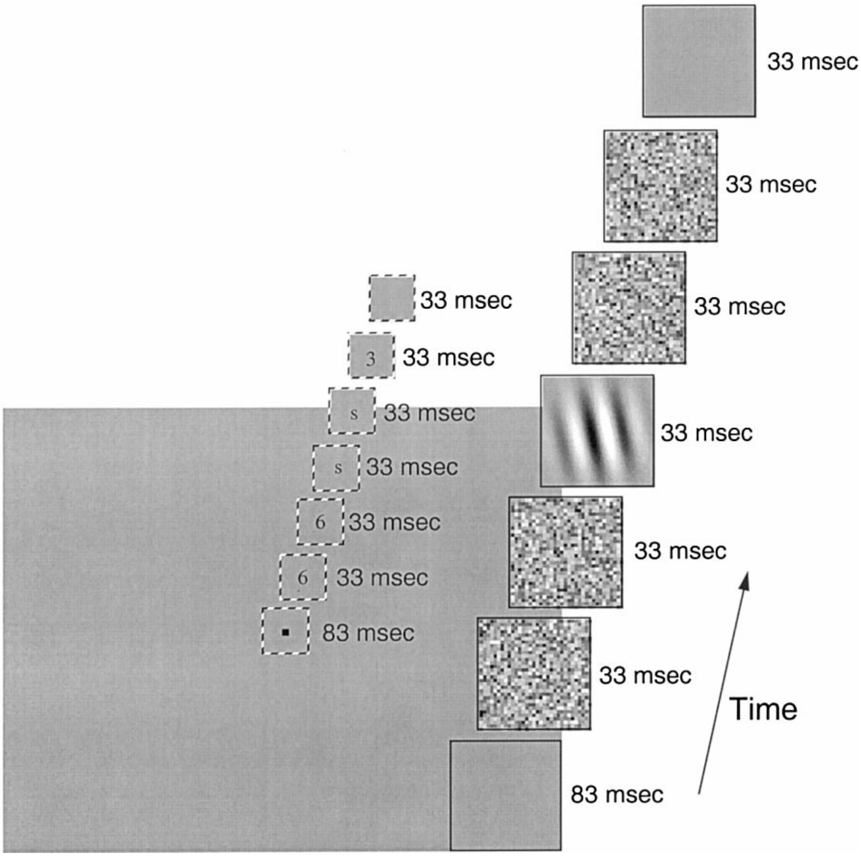

Fig. 4. A typical trial sequence. The observer detects whether an S or a 5 appeared in a rapidly presented digit/letter string at fixation (the central task). At the same time, noise and signal frames of the orientation identification task (top to the right or left) appear in the lower-right (training) quadrant. Transfer tasks included orientation identification in the corresponding positions of the upper-left and upper-right quadrants.

$$l(x,y) = l_0\left(1.0 + c\sin(2\pi f\,(x\cos\theta \pm y\sin\theta))\exp\left(-\frac{x^2+y^2}{2\sigma^2}\right)\right)$$

In this experiment, θ was $\pm 12°$. Each Gabor extended $1.54° \times 1.54°$, with a center frequency of $f =$ 2.3 cycle/deg, and a standard deviation $\sigma = 0.385°$. It was rendered on a 64×64 pixel grid. The mean luminance l_o was 71 cd/m^2. The maximum contrast of each Gabor varied according to a staircase tracking a criterion level of performance (see below). Viewing distance was approximately 76 cm. The initial training stimulus was displaced to the lower-right quadrant relative to fixation by 2.3° vertically and 3.1° horizontally. In subsequent transfer tests, the stimulus was displaced to the upper-left and -right quadrants relative to fixation.

The pixel graylevels for each external noise frame were constructed by sampling from a Gaussian distribution with mean 0 and variance depending on the amount of external noise for each noise condition. Noise frames had the same size as that of the signal frames with each pixel subtending $0.024° \times 0.024°$ visual angle. To guarantee that the external noise did conform to the Gaussian distribution, the maximum standard deviation of the noise was kept below 33% maximum achievable contrast. Each noise element consisted of a 2×2 pixel region.

The central task consisted of alphanumeric characters (times font) subtending approximately $0.144° \times 0.288°$ of visual angle. All displays were viewed binocularly with natural pupil at a viewing distance of approximately 76 cm in a dimly lighted room.

2.1.2. Apparatus

Signal and noise frames for the perceptual task were generated off-line using the HIPS image processing software (Landy, Cohen & Sperling, 1984a,b). Fixation and central task characters were generated online, and the precomputed signal and noise frames were displayed, using a program based on a software package (Runtime Library, 1988) on an Leading Technology monitor controlled by an AT-Vista videographics board in an IBM 486 PC computer. The monitor has a P4 phosphor, and the monitor was tuned to yield a square aspect ratio for horizontal and vertical pixels. A special circuit combined two output channels of the

AT-Vista board to produce 4096 distinct grey levels (12 bits).

Luminance calibration was performed both with psychophysical matching judgments and by measurement with a Photo Research Spectra Colorimeter (Model PR-650). The luminance of the monitor was 1 cd/m^2 when every pixel was assigned the minimum grey level, and was 144 cd/m^2 when every pixel was assigned the maximum grey level. The background was set at 71 cd/m^2. A lookup table was constructed to allow linear divisions of the entire range into 256 programmable grey levels. Finer grey levels are accomplished by interpolation.

2.1.3. Design

The central task, discriminating an S from a 5, was the same for all trials. Subject's threshold contrasts were estimated for the perceptual task at each external noise level. There were eight external noise levels (0, 0.02, 0.04, 0.08, 0.12, 0.16, 0.25, and 0.33). The experimental conditions were intermixed. Threshold contrasts were measured using a staircase procedure (Levitt, 1971) (see below), which estimates the contrast corresponding to a two alternative forced choice accuracy level of 0.793. There were 800 trials per session, consisting of 100 trials per staircase; two sessions were run per day. The perceptual task, discriminating the orientation of a Gabor patch, appeared in the lower-right quadrant for all training sessions. Data were collected for 8 days (16 sessions). Transfer data were also collected in which the perceptual task appeared in the upper-left and upper-right quadrants. The transfer conditions were tested for 2 days (four sessions) each.

2.1.4. Procedure

The display sequence of a typical trial is shown in Fig. 4. Following a subject keypress, a fixation display appeared for 0.5 s. The fixation display is a small central square. Frames for the central task and the peripheral perceptual task appeared during the same time interval. The central task display consisted of a sequence of three letters and numbers with the middle letter either an S or a 5 appearing at the same location as the fixation point. The perceptual task appeared in the lower-right quadrant of the monitor, and consisted of two frames of random noise, a signal frame with a Gabor patch tilted either left or right, and two additional frames of random noise. All noise samples in each trial are independent samples with the same contrast (variance). The noise is combined with the signal through temporal integration. Each frame appeared for 16.7 ms. After the stimulus sequence, the subject was cued for two responses: the central task (S vs. 5) and the peripheral perceptual task (left vs. right). Trials ended with a fixation display and auditory feedback (brief beeps after each correct response).

2.1.5. Staircase method

The psychophysical staircase procedure decreased signal contrast after three successive correct responses and increased signal contrast after every error (a three down–one up, or 3/1 staircase), which asymptotically estimates an accuracy level of 0.793 (d' of 1.634). Trials for the staircases associated with each condition were intermixed randomly. The number of reversals (where contrast changes) depends on the pattern of accuracy of the responses. The initial stepsize was adjusted for each external noise condition, and was decreased to half after the first reversal and again after the third reversal. The average contrast was calculated, after excluding the first two to three reversals, to yield an estimate of threshold contrast.

2.1.6. Observers

Observers were three undergraduate students naive to the purposes of the experiment. All had normal or corrected-to-normal vision.

2.2. Results

2.2.1. Central task

The visual conditions of the central task, discriminating an S from a 5, were identical throughout the experiment. The size and presentation rate of the central task was chosen to require fixation to allow adequate performance. Performance in the central task was reasonably good: a mean of 98% (range over sessions 91–99), 93% (87–96), and 80% (65–88) for observers DH, GM, and SP, respectively. The external noise level in the perceptual task did not effect accuracy on the central task (the effect of noise level was significant for observer GM, but that effect was very small, with differences of approximately 1%). Performance in the central task improved somewhat over sessions, with the largest improvement from the first to the second day, and relatively stable performance thereafter. With respect to perceptual learning, there was no systematic indication that accuracy on the central task was increasingly sacrificed to produce improved accuracy on the perceptual task over practice.

A contingency analysis based on the 2 × 2 table relating accuracy on the central task to accuracy on the peripheral perceptual task was performed to examine possible tradeoffs in attention between the central task and the perceptual task. If observers were trading accuracy in the central task, for accuracy in orientation discrimination, a negative relationship would obtain. Instead, the performance on the central task and orientation discrimination were positively related ($\chi^2(1)$ for N of 12 800 of 10.15, $P < 0.001$, 10.97, $P < 0.001$, and 1.764, n.s., for subjects DH, GM, and SP). Orientation discrimination was approximately 4% (6, 4, and 1%, respectively) more accurate on trials with a correct as

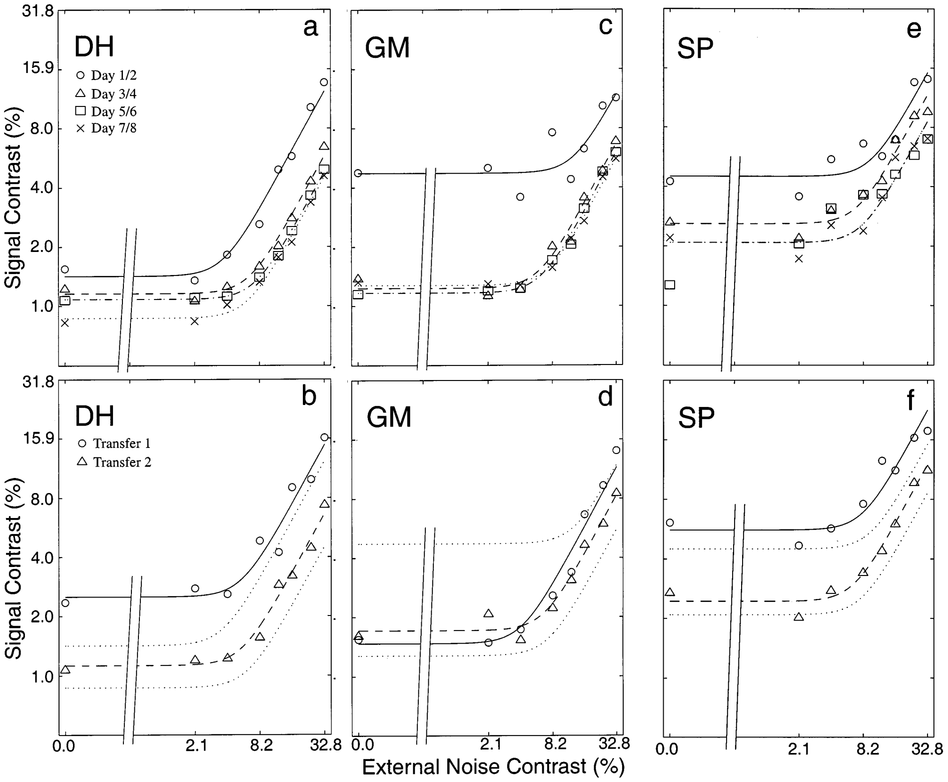

Fig. 5. Contrast threshold functions improve at all levels of external noise with practice over days for Experiment 1. The curves represent average performance over 2 day sets. (a), (c), and (e) show performance in the trained (lower-right) quadrant for three observers, while (b, d), and (f) show performance for transfer conditions for the corresponding observers. The smooth curves are fits of the PTM model. (Note that curves for day 5/6 and day 7/8 in panel (e) were virtually identical.) Transfer 1 tested the upper-left quadrant, while transfer 2 tested the upper-right quadrant. Dashed lines in (b, d), and (f) correspond to the initial and final performance in the original trained quadrant.

compared to an incorrect response on the central task. This pattern could arise from fluctuations in fatigue or alertness which affect both tasks similarly. Although a small negative relationship due to tradeoff, theoretically, might have been masked by positive correlations due to coupled fatigue and alertness effects, there is no evidence that attention tradeoffs provide an alternative explanation for perceptual learning improvements.

2.2.2. Orientation discrimination

The mechanisms of perceptual learning are studied with the perceptual task of orientation discrimination in the periphery. Fig. 5 shows threshold estimates (average contrast for criterion accuracy) for three observers as a function of external noise level. The variation in external noise produces curves which have the typical structure of TVC functions, flat at low levels of external noise and increasing at higher levels of external noise. Separate curves show performance over practice averaged over 2 day periods (four sessions). Data for the training location (lower-right quadrant) are shown on the top panels of the graph, while the data for the transfer conditions (upper-left and upper-right quadrants) are shown in the bottom panels[5]. The same data are regraphed in the more typical form as a function of practice in Fig. 6, with data from the transfer conditions shown on the right. In this case, the separate curves represent data for each of the external noise conditions.

The contrast required to achieve threshold performance increases with increasing external noise level (Fig. 5). Averaged over observers and practice, the thresholds range from about 2% for no external noise to about 8% for the highest external noise condition, a 412% increase in threshold[6]. There are a number of

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[5] The accuracy of performance averaged over trials contributing to the threshold estimates showed noticeable variation about the theoretical asymptotic accuracy of 0.793, as well as some evidence for bias in identification of direction (e.g. bias to say right or left). However, the sample sizes within a session were not large enough to justify a full analysis.

[6] Percent increase figures are calculated from the ratio of average contrasts between two conditions, in this case high noise and zero noise conditions. Approximate contrasts at threshold are rounded to the nearest percent. Percent increases or decreases are more precise.

ways to evaluate these effects statistically. An analysis of variance over observers found that the effect of the external noise manipulation was significant ($F[7, 14] = 105.11$, $P < 0.001$ on the log of threshold contrasts[7]). An analysis of variance for individual observers (using session within day as the random factor, see below) showed significant effects of noise level for each subject ($F[7, 7] = 556.89$, $P < 0.001$, $F[7, 7] = 166.04$, $P < 0.001$, $F[7, 7] = 25.42$, $P < 0.001$, for DH, GM, and SP, respectively, on log values). The quantitative form of the TVC functions is evaluated within the context of the PTM model in a subsequent section.

There is substantial improvement in the contrast required to achieve threshold performance over the 8 days of practice. Threshold, averaged over observers and noise level, drops from about 9% contrast on the first day of practice to about 3% contrast on the eighth day of practice, an improvement of approximately 70%. The largest improvements occurred early in practice, however continued practice appeared to be associated with incremental improvements. Contrast thresholds decreased significantly over the 8 days of practice ($F[7, 14] = 21.18$, $P < 0.001$ on log thresholds; $F[7, 7] = 556.89$, $P < 0.001$, $F[7, 7] = 2.15$, $P \approx 0.15$, and $F[7, 7] = 5.83$, $P < 0.02$, for individual subjects).

Examination of the data indicate that practice reduces threshold at all noise levels. For log contrast values, the interaction between noise level and day of practice was not significant ($F[49, 98] = 0.660$, $P \gg 0.10$), corresponding approximately (but not exactly) to vertical shifts on log axes of the performance functions over days. This observation is central in subsequent model analyses.

At a descriptive level, the data pattern is consistent either with the signature pattern of decreasing multiplicative internal noise over practice, or with a combination of increasing stimulus enhancement (additive internal noise suppression) and external noise exclusion over practice. This issue is also evaluated quantitatively within the PTM model in a subsequent section.

Sessions within a day did not differ reliably, nor did session interact with any other factor, in any analysis performed (over observers, within individual observers, on raw thresholds or log thresholds; all F's ≈ 1, $P > 0.10$). This result is consistent with previous observations of a number of authors that improvements with practice may require a period of consolidation (Karni & Sagi, 1993; Polat & Sagi, 1994) (but see Fiorentini & Berardi, 1981; Poggio, Fahle & Edelman, 1992 for examples of rapid learning). There is an ongoing discussion about whether learning requires a period of consolidation (overnight), or whether this pattern reflects more continuous learning which is offset by fatigue within a session or between sessions on the same day (Shiu & Pashler, 1992; Levi, Polat & Hu, 1997). Our result is consistent with prior reports, but cannot distinguish between these explanations.

2.2.3. Transfer of orientation discrimination

Karni and Sagi (1991, 1993) found that training on their perceptual task yielded improvements which were in large degree specific to the retinal position of training. Other researchers (Kapadia, Gilbert & Westheimer, 1994; Beard et al., 1995; Schoups, Vogels & Orban, 1995) have reported similar findings (but see Beard, Klein, Ahumada & Slotnick, 1996). Our results demonstrate in a simple orientation discrimination task the same pattern previously reported for texture discrimination tasks. The orientation discrimination task was trained in lower-right quadrant displays. Two transfer conditions were examined: upper-left quadrant displays (first) and upper-right quadrant displays (second). The thresholds on transfer locations, especially for the upper-left quadrant, are quite similar to those at the beginning of the training on the lower-right quadrant,

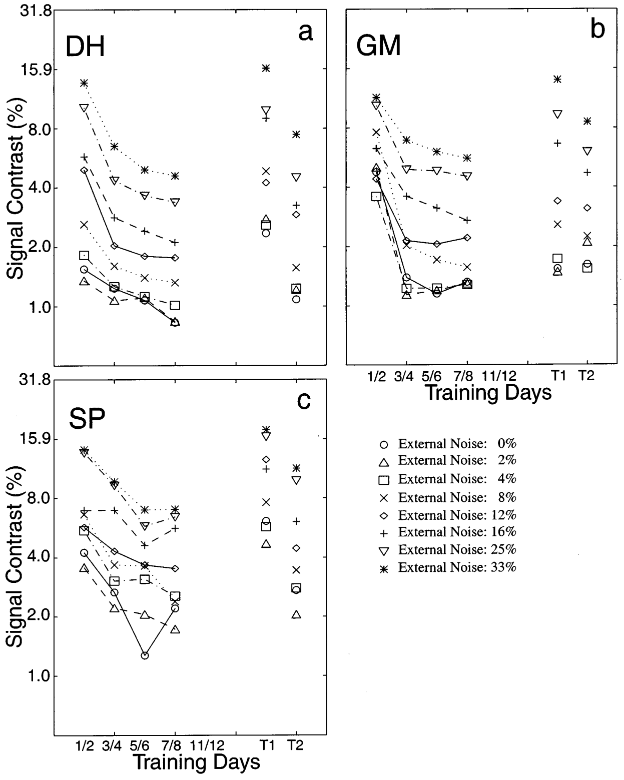

Fig. 6. The data of Experiment 1 graphed as a function of days of practice for each of three observers. Each curve represents data at one external noise level. T1 and T2 refer to transfer to the upper-left and upper-right quadrants, respectively.

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[7] Not surprisingly given the range of threshold values, there was some inhomogeneity of variance. Variances relevant for main effect tests were relatively homogeneous in the raw values; however, variances relevant to interactions showed more inhomogeneity, which is approximately corrected by taking the log. Analyses on raw values yielded essentially equivalent patterns of significance as those reported for log threshold analyses.

and significantly above the thresholds near the end of the 8 days of training (Figs. 5 and 6). Averaged over subjects, noise level and session, the threshold in initial performance was about 6.5% contrast, and at the end of performance was reduced to about 3% contrast. The threshold for the upper-left quadrant transfer condition was about 7% contrast (approximately equal to the initial level) and the threshold for the upper-right quadrant transfer condition was about 4 % contrast.

The thresholds for the transfer tasks and the initial sessions of the original task were generally similar. (Observer GM showed better performance on transfer 1 than other observers in these experiments, while observers DH and SP showed transfer 1 performance worse than initial performance. These may reflect genuine differences between observers or may merely reflect statistical variations.) Analyses over observers were performed on 2-day data groups[8]. The initial performance and the two transfer conditions differed only marginally ($F[2, 4] = 6.13$, $P \approx 0.06$ on log thresholds). This marginal difference reflected slightly improved performance of the transfer to the upper-right quadrant, which yielded a pattern of occasional significance compared with either initial performance or the upper-left quadrant transfer in both the group and individual subject data. In total, transfer performance was generally similar to initial, unpracticed task performance, although the upper-right quadrant transfer showed some benefit of practice. Whether this reflects partial transfer between retinal locations within a hemifield, or improvements associated with learning to learn (Liu & Vaina, 1998) cannot be determined in the current data because the same-hemifield transfer was always tested second.

Transfer performance was always worse than the final, practiced performance on the original retinal location. Final after-practice performance and the two transfer conditions differed significantly ($F[2, 4] = 14.30$, $P \approx 0.01$ on log thresholds). Final performance on the lower-right quadrant (standard) was better than the transfer to the upper-left quadrant ($F[1, 2] = 19.88$, $P < 0.05$ on log thresholds) and better than the transfer to the upper-right quadrant ($F[1, 2] = 141.67$, $P < 0.01$ on log thresholds). This pattern was replicated in the individual subject analyses.

In total, the pattern of transfer demonstrated practice improvements on the orientation discrimination task which generally showed substantial specificity to the retinal location. This fact is important, because similar findings have previously been used to argue for a basis of perceptual learning in retinally specific neural plasticity.

2.2.4. PTM model analysis

Thresholds for the orientation discrimination task show improvements with practice at all levels of external noise. At the system level, this pattern is qualitatively consistent with improvements in (multiplicative) internal noise suppression or with some mixture of improved stimulus enhancement (additive internal noise suppression) and improved external noise exclusion or filtering, or a mixture of all three.

The data were quantitatively modeled using the equation (in log form, Eq. (3)) for mechanisms of perceptual learning, as developed earlier. In the model, log threshold contrast ($\log(c_\tau)$) is a function of: d', the chosen threshold level; N_{ext}, the level of external noise in a display condition; N_m, the power of multiplicative internal noise; N_a, the power of additive internal noise; β, the gain on a signal-valued stimulus; and nonlinearity parameters γ_1 and γ_2. Finally, there are multipliers on multiplicative internal noise (A_m); on additive internal noise (A_a); and on the width of the external noise filter (A_f). The levels of N_{ext} and the criterion d' values are selected by the experimenter. The remaining parameters are free to vary in a fit of the model to data for each observer. The values of N_a, N_m, β (in this case), and nonlinearity parameters γ_1 and γ_2, are the same for all conditions in the experiment. Only the values of $A_.$ vary from condition to condition. The $A_.$ parameters are attenuators which capture the improvements in performance with practice. Values of the $A_.$'s are (by definition) set to one for the first (unpracticed) session(s); hence performance after various amounts of practice is referred back to the initial level of performance.

The model was fit to the data with a procedure implemented in Matlab. Each observer's data were fit separately. Model parameters were adjusted using a gradient descent method so as to minimize the error function, the sum of the squared differences between the predicted ($\log c_\tau^{\text{theory}}$) and observed ($\log c_\tau^{\text{obs}}$) threshold contrasts. The goodness-of-fit is evaluated by the r^2 measure of percent variance accounted for by the model (Eq. (4)):

$$r^2 = 1.0 - \frac{\sum (\log(c_\tau^{\text{theory}}) - \log(c_\tau))^2}{\sum (\log(c_\tau) - \text{mean}(\log(c_\tau)))^2} \tag{4}$$

where Σ and mean ( ) apply to all data points for a particular subject.

In order to evaluate the mechanism(s) underlying perceptual improvement, versions of the model with different mechanisms of improvement with learning ($A_.$ parameters) must be compared. Models which are nested (whose parameters are proper subsets or supersets of one another) may be statistically compared by

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[8] Subject DH performed only 1 day of tests on each transfer, so his analyses were performed on single day sets. His single days were replicated with noise for the group analyses.

application of an F-test comparing a fuller to a reduced model (Eq. (5)):

$$F(\mathrm{d}f_1, \mathrm{d}f_2) = \frac{(r^2_{\text{full}} - r^2_{\text{reduced}})/\mathrm{d}f_1}{(1 - r^2_{\text{full}})/\mathrm{d}f_2} \tag{5}$$

where $\mathrm{d}f_1 = k_{\text{full}} - k_{\text{reduced}}$, and $\mathrm{d}f_2 = N - k_{\text{full}} - 1$. The k's are the number of parameters in each model, and N is the number of predicted data points (Wannacott & Wonnacott, 1981).

The PTM model was fit to the 2-day average data shown in Figs. 5 and 6. Although nonlinearities were present in this situation, the Experiment 1 data were not sufficient to constrain the estimates of nonlinearity. (Lu and Dosher (1998a) found evidence for nonlinearity in the non-unit slope of the high noise region of the external noise functions; nonlinearities are revealed for the displays in Experiment 2 by data at two d' criteria.) The fits we describe here eliminate nonlinearities (set $\gamma = 1$). The conclusions, however, are essentially unchanged by the consideration of nonlinearities (see Section 4.2.4). A full lattice of nested model fits were performed. The fully saturated linear model has 12 free parameters, including N_m, N_a, and β, and nine perceptual learning attenuation parameters $A_.$ (A_m, A_a, and A_f for each of days 3/4, 5/6, and 7/8; days 1/2 set at 1.0). The minimal model, corresponding to no perceptual learning, requires only the first three free parameters. The lattice explores all models in between. The minimal model fits the same function to all four performance curves in Fig. 5. The quality-of-fit of the models is summarized by the r^2. The minimal model produces midrange r^2 ($r^2 = 0.777$, 0.550, 0.687, respectively, for DH, GM, and SP) because it accounts for the general level of performance and for the substantial effects of external noise level.

Any model which allowed attentuation parameters (A_f, A_a, or A_m) to vary with practice significantly improved the quality of the fits. No single mechanism of perceptual learning was able to fully account for the pattern of improvement with practice. One or more mixture model(s) fit the data significantly better ($P < 0.01$) than pure stimulus enhancement (additive internal noise suppression), external noise exclusion, or (multiplicative) internal noise suppression. Therefore, perceptual learning was accomplished by a mixture of mechanisms. Unfortunately, while we could unambiguously determine that more than one mechanism was necessary to explain the improvements in performance with perceptual learning, the precise mechanism mixture could not be determined. Not only were a number of the mixture models statistically indiscriminable, several produced *exactly* the same maximum r^2 as the fully saturated model (maximum r^2 of 0.9879 for three mixture models for DH; of 0.9672 for four mixture models for GH; and of 0.9160 for three mixture models for SP). These mixtures are true aliases for one another: fits of equivalent quality result from rather different parameter values. The data of Experiment 1 and a set of more constrained parameter estimates are reconsidered after estimating nonlinearity parameters from Experiment 2.

2.3. Discussion

Perceptual learning produced substantial improvements over 8 days of practice, and these improvements were in large degree specific to the trained retinal location. Tradeoffs between orientation discrimination and central task performance were not a contaminating factor. Perceptual learning improved performance at both low and high levels of external noise, by an approximately equal amount on log contrast axes. This pattern of perceptual learning reflects a mixture of mechanisms. However, in this case we cannot determine the exact nature of the mixture, or the exact nature of nonlinearities, without further constraints on the model by data. The discrimination of mixtures presents a challenge. One approach to this challenge is described in Section 3.

3. Discriminating mechanism mixtures

The identification of mixtures of stimulus enchancement (additive internal noise suppression), external noise exclusion, and multiplicative internal noise suppression is important to a full understanding of the perceptual mechanisms underlying performance whenever two conditions exhibit differences at both high and low levels of noise in the environment. One method of discriminating such mechanism mixtures is based on the phenomenon shown in Fig. 7, which illustrates predictions of the PTM model for contrasts at *two different* thresholds for each of the signature mechanism patterns shown in Fig. 3.

A higher level of threshold performance, for example a d' of 1.5 instead of 1.0, requires higher contrast signals to achieve. Fig. 7 illustrates contrast threshold differences at lower (dashed lines) and higher (solid lines) criterion threshold values between conditions differing in stimulus enhancement (changed A_a), in external noise exclusion (changed A_f), and in multiplicative internal noise reduction (changed A_m). For conditions differing only in stimulus enhancement (additive internal noise reduction) (Fig. 7a) or only in external noise exclusion (Fig. 7b), the size of the effect is the same (on the log contrast axis) at both the higher, more stringent threshold and the lower, less stringent threshold. This property follows from Eq. (3), in which the threshold (criterion) d' occurs only in the second term, $-(1/2\gamma)\log(1/d'^2 - A_m^2(k)N_m^2)$. So long as A_m and γ are constant, all differences in criterion produce a vertical

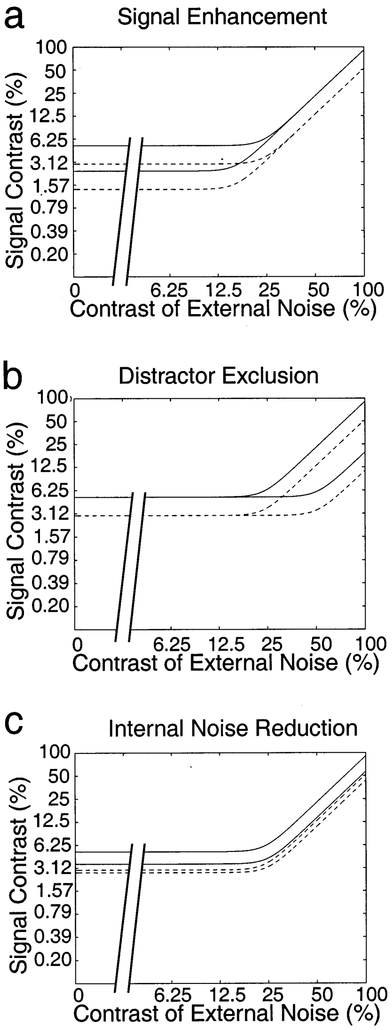

Fig. 7. Patterns of stimulus enhancement, distractor exclusion, and internal noise reduction for two different criterion d' levels. Multiple d' criteria allow the discrimination of mechanism mixtures; stimulus enhancement and external noise exclusion produce condition differences that are vertically shifted relative to one another on log axes (have a constant contrast ratio), whereas multiplicative noise reduction predicts larger condition differences at high than low criteria.

shift on log axes, independent of changes in either A_a or A_f, which appear in only the first term of Eq. (3). This shift-invariance on log axes is labeled the *criterion-independent effect size property* of stimulus enhancement and external noise exclusion.

However, threshold contrast differences between two conditions at lower and higher criterion threshold values are strongly dependent upon criterion level in the case where conditions differ in internal multiplicative noise reduction. In Eq. (3), changes in A_m impact the second term, in which criterion d' and A_m interact. This is labelled the *criterion-dependent effect size property* of multiplicative noise reduction.

The differential pattern of increases in threshold contrasts for more stringent criteria compared to less stringent criteria provide a means to distinguish between mechanism mixtures in the PTM model. The measurement of two or more sets of threshold contrasts places extremely strong constraints on the fits of the PTM model which are key to identifying mixtures. Measurement of performance at more than one performance criterion is the strategy for disambiguation of mechanism mixtures followed in Experiment 2.

The additional information provided by the measurement of two or more sets of threshold contrasts in the perceptual learning paradigm also serves to constrain the estimates of visual system nonlinearities. The ratios between performance at several threshold levels can be used to estimate the nonlinearity parameters. The independence of these ratios over external noise level provides a consistency test of the model form[9]. The departure of the ratios from the ratio of d' mandates $\gamma \neq 1$ and constrains the estimate of the nonlinearity. Finally, the equality of these ratios over days of practice indicate a constant γ and A_m (see above). The theoretical development of strong ratio tests for nonlinearity and experimental applications to identification and detection tasks are described in detail in Lu and Dosher (1999).

4. Experiment 2

The goals of this experiment were to replicate the finding that perceptual learning improves performance in both high and low external noise, and to more fully characterize the nature of the mechanism (or mixture of mechanisms) mediating learning using a two criterion, or two threshold, protocol.

4.1. Method

This experiment is identical to Experiment 1 except that two thresholds were estimated for each condition. Experiment 1 used a psychophysical staircase procedure which decreased signal contrast after three successive correct responses and increased signal contrast after every error (a three-down one-up or 3/1 staircase); which tracked a two alternative forced choice threshold value of 0.793 proportion correct (d' of 1.634). In this Experiment, an additional staircase was used which decreased signal contrast after two successive correct responses and increased signal contrast after every error (a two-down, one-up or 2/1 staircase); this tracked a two alternative forced choice threshold value of 0.707 proportion correct (d' of 1.089).

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[9] In particular, the constancy of threshold ratio at two d' criterion levels over changes in external noise is consistent with the $N_m^2(\beta^{2\gamma}c^{2\gamma} + N_{\text{ext}}^{2\gamma})$ form of multiplicative noise which eliminates cross terms.

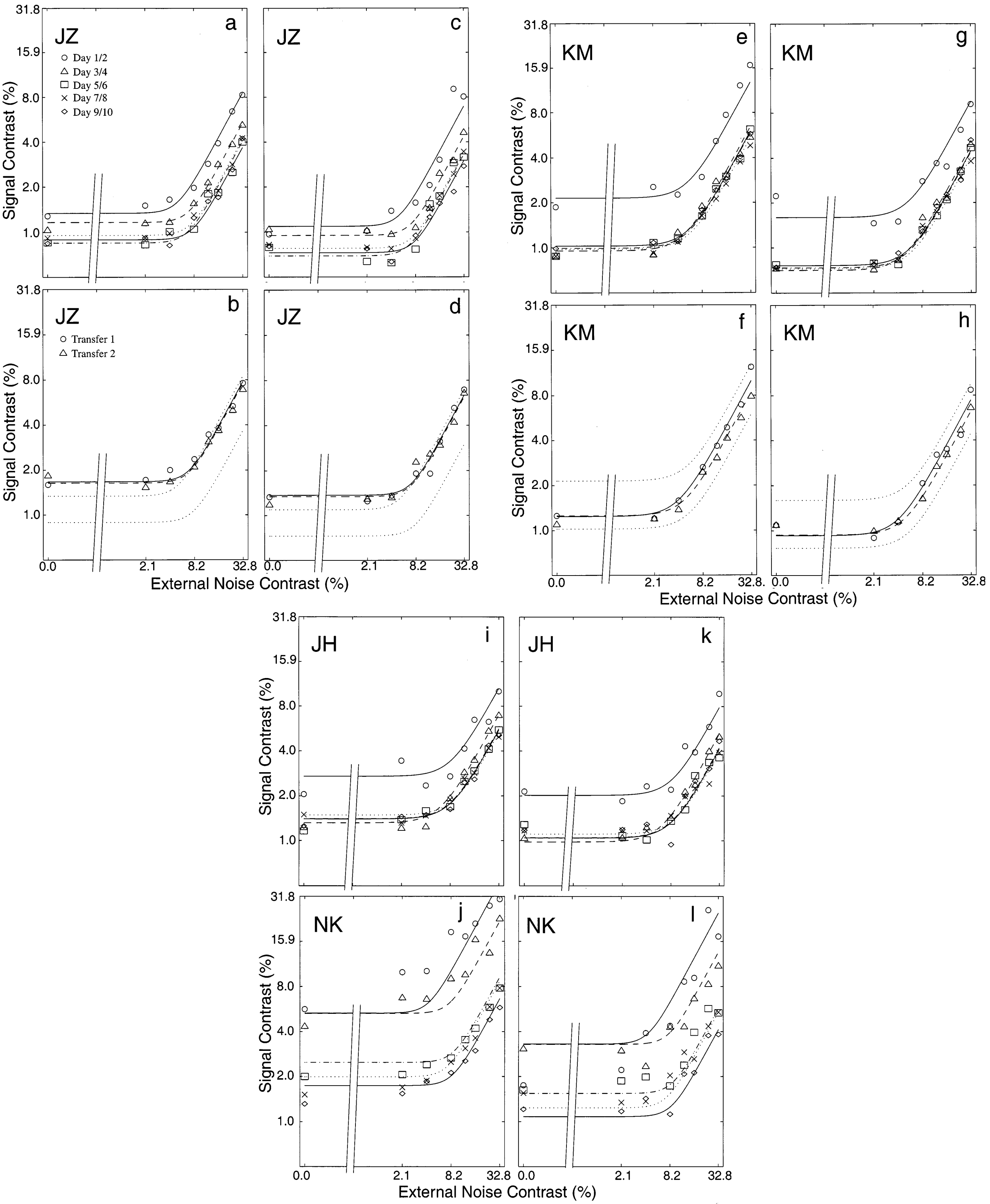

Fig. 8. Contrast threshold functions improve at all levels of external noise with practice over days for Experiment 2. The curves represent average performance over 2 day sets. Curves correspond to days of practice. Panels (a, e, i), and (j) present the training performance from the high criterion staircases for four observers, and (c, g, k), and (l) present the corresponding data from the lower criterion staircases. Panels (b, f) and (d, h) present the transfer data for two of the observers. Smooth curves are the fits of the PTM model. Dashed lines in (b, d, f), and (h) correspond to the initial and final performance in the original trained quadrant.

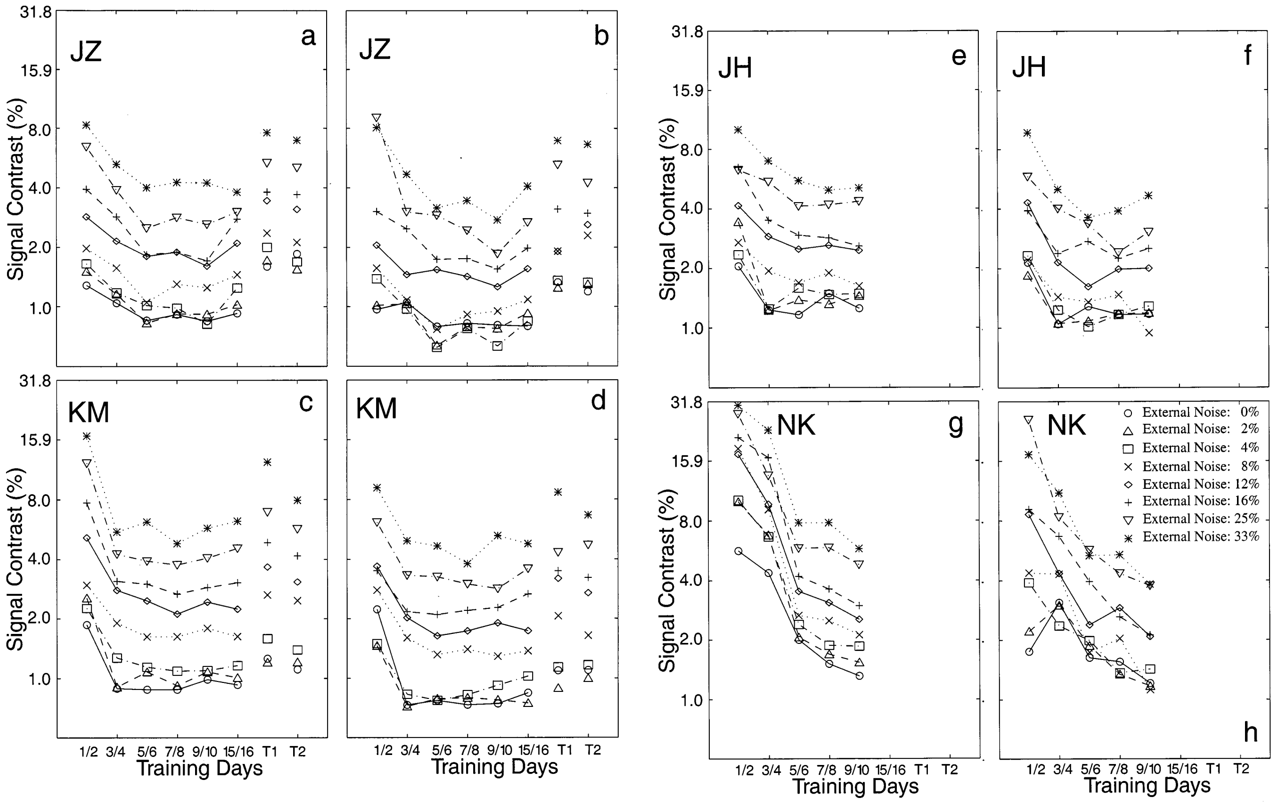

Fig. 9. The data of Experiment 1 graphed as a function of days of practice for each of four observers. Each curve represents data at one external noise level. Data from the higher criterion staircases are shown in panels (a, c, e), and (g), and from the lower criterion staircases in panels (b, d, f), and (h). T1 and T2 refer to transfer to the upper-left and upper-right quadrants, respectively.

Experiment 2 differed from Experiment 1 in several other ways. Experiment 2 was run in a single session per day, with 1440 trials per session, consisting of 100 trials for each 3/1 staircase and 80 trials for each 2/1 staircase. Finally, the starting values for sessions after the first one were set equal to the final values from the previous session, with stepsize set to 0.9 of the initial stepsize of the previous session[10].

4.1.1. Observers

The observers were four undergraduate students with normal or corrected to normal vision and naive to the purposes of the experiment. Subjects JH and NK did not participate in transfer condition tests due to time constraints on their participation.

4.2. Results

4.2.1. Central task

Performance on the central task, discriminating an S from a 5, was reasonably high, with an accuracy level of 89% (range over sessions 85–90), (88 (84–90), 89 (85–91), 94 (89–96), and 84 (69–91), for JH, JZ, KM, and NK, respectively). Accuracy was very similar across sessions (with the exception of NK, who had lower accuracies for the first two sessions). Accuracy of the central task was essentially unaffected by the external noise level of the orientation discrimination task.

As in the previous experiment, the contingency analysis of these data provided no evidence of attentional tradeoffs between the central task and the orientation discrimination task. The accuracy of orientation discrimination was approximately 9% (7, 10, 7, and 12% for JH, JZ, KM, and NK, respectively) higher for trials with accurate compared to inaccurate central task responses ($\chi^2(1)$ for N of 14400 of 43.67, 77.94, 21.21, and 154.22, all $P < 0.001$, respectively). Overall, the pattern of accuracy and contingency is similar to that of Experiment 1.

4.2.2. Orientation discrimination

The data for the orientation discrimination task are again shown in two formats. Fig. 8 shows threshold contrasts as a function of external noise level, and Fig. 9 shows threshold contrasts as a function of days of practice. The data for the two different thresholds are shown in separate panels.

As expected, the less stringent staircase (2/1), which tracks an asymptotic accuracy of 0.707, required lower

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[10] Starting values for staircases estimating thresholds for modestly differing conditions are sometimes chosen randomly within a range. In this case, performance differences over days were so large that using a common range for starting values would have led to estimation instability.

contrasts than the more stringent staircase (3/1), which tracks an asymptotic accuracy of 0.793. Averaged over observers and conditions, the contrasts were about 3 and 4%, a 46% proportional increase from the lower to the higher threshold. This was significant in the analysis of variance over observers on log of contrast thresholds ($F[1, 3] = 22.139$, $P < 0.01$) and for each observer individually ($F[1, 3] = 94.33$, 176.42, 57.70, and 163.91, all $P < 0.001$, for JH, JZ, KM, and NK, respectively).

The contrast required to achieve threshold performance increases with increasing external noise. Averaged over observers, criterion level and practice, the thresholds range from about 2 to 7% contrast, and increase of approximately 500%, from the no-noise to highest external noise condition. The external noise manipulation was significant in an analysis of variance over observers ($F[7, 21] = 195.70$, $P < 0.001$, on log threshold contrast), and for each observer ($F[7, 35] = 224.43$, 209.42, 503.30, and 192.38, all $P < 0.001$, for JH, JZ, KM, and NK, respectively).

As in Experiment 1, there is a substantial decrease in the contrast required to achieve threshold performance over the 10 days of practice. Thresholds, averaged over observers, criterion level, and noise condition, improved by about 67%, from about 7% contrast to 2% contrast. Individual observer improvements were generally comparable. As before, improvements were largest early in practice[11]. An analysis of variance over observers (criterion level, noise condition, 2-day practice set, and day within set as factors) showed a significant improvement over practice sets (shown in Fig. 8 as day 1/2, day 3/4, ...) ($F[4, 12] = 9.35$, $P < 0.001$) and for days within practice sets ($F[1, 3] = 13.12$, $P < 0.05$). Analyses for individual observers similarly showed significant effects of practice set ($F[4, 12] = 5.01$, 36.34, 6.02, and 33.58, all $P < 0.01$, for JH, JZ, KM, and NK, respectively[12]).

4.2.3. Transfer of orientation discrimination

Improvements due to practice in the lower-right quadrant task did not transfer substantially to task performance in the transfer quadrants. Thresholds for the transfer tasks are higher than those for the practiced levels of the original task. Only observers JZ and KM participated in the transfer conditions. The pattern was equivalent for the two observers: neither transfer condition differed significantly from the performance in the first practice set of the standard training (all $F < 1.0$); and both transfer conditions were reliably above the performance in the last practice set (day 9/10) ($F[1, 1]$ of 138.033, $P < 0.05$ and 150.03, $P < 0.05$ for JZ; $F[1, 1]$ of 1069.28, $P < 0.01$ and 18.63, $P \approx 0.10$ for KM). In total, as in Experiment 1, the pattern of transfer showed practice improvements in the orientation discrimination task which were reasonably specific to the retinal location.

4.2.4. PTM model analysis

Practice improved threshold contrasts for the orientation discrimination task at all levels of external noise. In Experiment 1, no single signature mechanism by itself accounted for improvements in orientation discrimination with practice. However, with single threshold data, the mixture of mechanisms underlying the improvements could not be unambiguously determined. In Experiment 2, performance at two thresholds provided strong constraints on the model that allow the discrimination of mechanism mixtures. As before, the PTM model was applied to the data from 2-day averages, shown in Fig. 8. The data from the two thresholds (staircases) are shown in separate panels.

Models that constrained either γ_1 or γ_2 or both to 1.0 were easily rejected. The data from the two d' threshold conditions exhibit strong and constraining regularities (see Lu & Dosher, 1999 for a related analysis). In the current data, the ratio of contrasts at the two threshold levels was approximately constant over noise level. This corresponds to the observation that the threshold curves for the higher criterion (Fig. 7a) and the threshold curves for the lower criterion (Fig. 7b) are approximately shifted versions of one another on the log contrast axis. The only term in Eq. (3) that is a function of threshold d' is $-1/2\gamma \log(1/d'^2 - A_m^2(k)N_m^2)$. In the absence of multiplicative noise and nonlinearity ($N_m = 0$, $\gamma = 1$), the ratio of threshold contrasts for two d' criteria is just the ratio of the two d's (Lu and Dosher, 1999) in this case 1.5, corresponding to a difference of 0.405 in the log form. To accomodate the observed value of the ratio (1.27, 1.75, 1.23, 1.35 for JH, NK, JZ, and KM, respectively), a nonlinearity is required. The threshold ratio is predicted to be the same over all external noise levels, which follows from the absence of N_{ext} in the Eq. (3) term above. This prediction forms an internal test of the model which was validated in the current data in the independence of the observed threshold ratio over noise level (all $P > 0.10$). Similarly, the threshold ratios were essentially constant over days of practice. (The only exception was the day 1/2 data of NK, which exhibited a slightly higher ratio. These data were, however, extremely noisy, and so this possible difference should be viewed with caution.) The fact that the threshold ratios were essentially equal over practice requires that nonlinearity in transducer functions and the value of multiplicative

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[11] Apparent minor differences in the rate of improvement as a function of practice in Experiments 1 and 2 may reflect differences in the training schedule or in differential experience with examples at different thresholds. However, these experiments were not designed to allow serious comparisons.

[12] These analyses used a composite of days within practice set and criterion level to produce a random factor (four levels).

Table 1
Parameter estimates for the A_a–A_f mixture model[a]

Parameter	Experiment 2				Experiment 1		
	JH	JZ	KM	NK	DH	GM	SP
γ	1.381	1.999	1.370	2.048	1.700	1.700	1.700
N_m	0.020	0.042	0.001	0.545	0.019	0.015	0.173
N_a	0.033	0.003	0.019	0.002	0.004	0.032	0.019
β	4.522	4.977	3.702	1.649	3.579	3.756	3.018
A_a (2)	0.369	0.755	0.329	0.992	0.705	0.101	0.393
A_a (3)	0.403	0.401	0.347	0.210	0.630	0.093	0.270
A_a(4)	0.436	0.507	0.339	0.133	0.433	0.108	0.271
A_a (5)	0.401	0.443	0.363	0.101	–	–	–
A_f (2)	0.666	0.628	0.501	0.546	0.467	0.563	0.775
A_f (3)	0.535	0.475	0.459	0.231	0.387	0.511	0.565
A_f (4)	0.502	0.491	0.423	0.218	0.366	0.474	0.568
A_f (5)	0.524	0.432	0.467	0.166	–	–	–
r^2	0.957	0.967	0.977	0.929	0.992	0.971	0.899
R^2	0.950	0.961	0.974	0.919	0.989	0.961	0.863
A_a (ul)	–	1.583	0.474	–	2.629	0.137	1.457
A_f (ul)	–	0.918	0.781	–	1.206	0.982	1.492
A_a (ur)	–	1.499	0.481	–	0.675	0.177	0.354
A_f (ur)	–	0.893	0.655	–	0.539	0.708	0.793

[a] Assumed values, $A_a\,(1) = A_f\,(1) = A_m(k) = 1.0$. The value $\gamma = 1.700$ for subjects in Experiment 1 was set by the average γ from Experiment 2.

noise, γ and N_m, remain unchanged over practice. This observation contradicts the criterion-dependent effect size property of the multiplicative noise reduction mechanism. It is this strong ratio constraint between thresholds of the two criterion levels which rules out multiplicative internal noise reduction as a mechanism of perceptual learning in these data. The constancy of this ratio over days also rules out significant changes in the nonlinearity γ with perceptual learning.

The models that assumed a single γ ($\gamma = \gamma_1 = \gamma_2$) yielded good fits to the data. Estimating independent γ_1 and γ_2 neither improved the fits nor altered the conclusions. Hence, we report in detail only the single γ fits. A full lattice of nested model fits was performed. The fully saturated model has 16 free parameters, γ, N_m, N_a, β and 12 $A_.$ (three parameters, A_f, A_a, and A_m, for each curve after the first day). The minimal model has four free parameters (γ, N_m, N_a, and β); this fits the same function to all five curves within each d' criterion set ($r^2 = 0.804$, 0.774, 0.787, and 0.430, respectively, for JZ, JH, KM, and NK; compare to full model r^2 in Table 1).

Consistent with the ratio tests described above, in no case did allowing multiplicative internal noise reduction (A_m) to vary with practice systematically improve the fit of the model in comparison to the same model without changes in multiplicative noise reduction. Allowing *either* changes in external noise exclusion (A_f) with practice *or* changes in stimulus enhancement (A_a) with practice improved the fit relative to the minimal model ($P < 0.01$ for all observers). Stimulus enhancement improves performance only at low levels of external noise and external noise exclusion improves performance only at high levels of external noise. However, practice improved performance at *all* levels of external noise. A combination of the two mechanisms accounts for perceptual learning better than either alone ($F[4, 67] =$ 54.60 and 12.03, $P < 0.01$, for JZ; 24.75 and 21.37, $P < 0.01$, for JH; 54.64 and 34.12, $P < 0.01$, for KM; and 29.73 and 15.88, $P < 0.01$, for NK; for comparisons to A_a and A_f changes alone).

The parameter values for the model that accounts for improvement in performance with practice by a combination of improved external noise exclusion and improved stimulus enhancement (reduced additive internal noise) are listed in Table 1. The $A_f(k)$ and $A_a(k)$ correspond to multipliers for days where the value of 1.0 for day 1/2 serves as a baseline. Values less than 1.0 represent an improvement in performance.

Each observer in this experiment exhibited some nonlinearity (γ of 1.99, 1.38, 1.36, 2.04, respectively for JZ, JH, KM, and NK). The average γ of 1.7 was used to constrain a reanalysis of the data from Experiment 1. These constrained model fits of Experiment 1 were completely consistent with the model fits of Experiment 2. The resulting parameter estimates are also listed in Table 1.

The perceptual learning parameters $A_a(k)$ and $A_f(k)$ for different observers (see Table 1) essentially quantify percentage reductions in the performance-limiting noise. Over observers, perceptual learning improves the exclusion of external noise (A_f) by a factor of two or more while simultaneously reducing additive internal noise (A_a) (improved stimulus enhancement) by 50% or more.

Performance on transfer tests for quadrants other than the lower-right (trained) quadrant were fit separately by estimating A_a and A_f assuming values of γ, N_a and β estimated from the main perceptual learning data. These values are listed at the bottom of Table 1. Transfer performance which was equal to that of the first training set (days 1/2) would yield A_a and A_f estimates of 1.0. The estimated parameters for the transfer data are consistent with the statistical analysis of the data provided previously. Multiplier values for the transfer conditions were without exception larger than the comparable multipliers for the last practice set on the standard quadrant, and with one exception were larger that those of day 2.

4.3. Discussion

Perceptual learning produced substantial location-specific improvements in peripheral orientation identification over the ten days of practice. There is no evidence that central task performance traded off with performance on the peripheral task. Orientation identification improved with practice at both low and high levels of external noise, corresponding to improvements in both external noise exclusion and stimulus enhancement. An analysis of Experiment 1 using nonlinearity estimated from Experiment 2 yielded consistent results. Furthermore, evaluating performance at two (or more) criterion threshold levels was an effective method of providing strong constraints on models of perceptual learning.

5. General discussion

5.1. Perceptual learning in external noise

The current experiments measured perceptual learning associated with practice over days in an orientation identification task. Perceptual learning was largely specific to the visual quadrant in which the training occurred. Specificity of learning to the trained position has been used in previous research to argue that perceptual learning reflects neural plasticity in adult visual system (e.g. Karni & Sagi, 1991, 1993). Our data document the mechanisms of perceptual learning in our task and suggest hypotheses about the functional level of the observed plasticity.

Previous investigations in humans have generally studied perceptual learning only in noiseless environments. These experiments are the first to systematically apply an external noise paradigm in perceptual learning. Perceptual learning in this task improved performance over a wide range of levels of environmental or external noise in the displays, indicating a mixture of learning mechanisms. In contrast, manipulations of spatial attention have been shown to selectively impact only low noise regions (Dosher & Lu, 1997; Lu & Dosher, 1998a) under some circumstances and only high noise regions (Lu & Dosher, 1998b) under others. Quantification of perceptual learning in the presence of environmental noise is of both empirical and theoretical interest.

5.2. PTM model of perceptual learning

The perceptual template model (PTM) describes the performance of the observer in terms of a perceptual template, a nonlinear transducer function, multiplicative internal noise, and additive internal noise. The PTM considers the observer as a whole system. Improvements in performance with perceptual learning (or due to attentional state) are characterized as stimulus enhancement (equivalently, additive internal noise suppression), external noise exclusion, multiplicative internal noise suppression, or more generally, as mixtures of these mechanisms.

The PTM model and its extension to multiple criterion levels allowed strong identification of the effects of perceptual learning. Perceptual learning in the orientation discrimination tasks reflected: (1) The observer's ability to exclude external noise, by changing the shape of the perceptual filter, improved with practice; (2) The observer's ability to enhance the stimulus, or equivalently to reduce additive internal noise, improved with practice. In the current experiments, perceptual learning narrowed the perceptual filter approximately by a factor of two or more, and reduced additive internal noise by 50% or more. The ratio of contrast threshold for the two criterion levels was essentially constant over levels of external noise, an internal consistency constraint of the model, and over days of practice, a constraint that eliminates significant reductions in internal multiplicative noise as a mechanism of improvement. The approximate constancy of this ratio over days of practice also rules out systematic changes in nonlinearity as a mechanism of learning. That neither multiplicative noise nor transduction nonlinearity change over days suggests that contrast gain control properties of the system remain essentially constant.

Our results are consistent with previous results on transfer of perceptual learning, but go far beyond those findings. They identify two mechanisms of improvement. At this point, the generality of the finding that perceptual learning reflects improvements in stimulus enhancement and in external noise exclusion is unknown. These experiments are the first to apply the external noise paradigm to reveal the mechanisms of improvement with perceptual learning. Further experimentation on a range of perceptual tasks is required to further specify the nature of perceptual learning in other contexts.

5.3. Variants of the PTM model

This section, which may be omitted, considers technical variations of the PTM model: the model conclusions are quite general. The PTM model of Fig. 2 shows additive noise following multiplicative noise and nonlinearities. Yet some forms of noise considered by earlier investigators, such as photon noise or sampling noise (de Vries, 1943; Rose, 1948; Pelli, 1981; Liu & Vaina, 1998) plausibly occur early in the visual system, possibly preceding the perceptual template or filter. Indeed, there are three places in the model where additive noise might be introduced: (1) prior to the perceptual template; (2) after the perceptual template but before nonlinearity and multiplicative noise; or (3) after nonlinearity and multiplicative noise. Although these locations of additive noise may correspond to different physiological possibilities, Appendix A demonstrates that, at the level of functional equations, additive noise in locations (1) and (2) may be equivalently rewritten as an additive noise in location (3), the form considered throughout this paper. In practical terms, Appendix A shows that all additive noise may be collected together and expressed as one noise in location (3)[13]. This holds at the systems level of the current analysis, although other methods or approaches may provide additional information. One consequence is that estimated additive internal noise in the current PTM model may reflect a combination of locations of additive noise. The advantage of this PIM form is that it yields independent estimates of external noise exclusion and additive internal noise reductions.

However, additive internal noise in location (3), cannot in general be rewritten as noise in location (1) (Appendix A). In particular, if all internal additive noise reflected performance limits prior to the template, then the amount of additive noise reduction (stimulus enhancement) and the amount of external noise exclusion would be required to be exactly coupled. Although the two are loosely coupled in this case of perceptual learning, they are not perfectly coupled in the manner required by a model with additive noise in location (1), prior to the template. In the case of our Experiment 2 data where the model form is constrained by two d' threshold levels, this 'early noise' model was tested as a nested form of the full PIM model ($A_a = A_f$), and was rejected ($P < 0.001$) for all observers. This observation is crucial because it allows us to rule out a model in which all additive noise is early, and perceptual learning consists only in retuning the perceptual template. Although this is in some sense a modest constraint on the location of processing limits represented by additive internal noise, previous treatments of limiting noise properties provided no constraints on early versus late noise contributions (Pelli, 1981; Ahumada & Watson, 1985).

Considering the current data in isolation, strictly speaking the conclusion is that the additive noise reductions cannot be solely early, but might include both early and late components. In fact, we believe that the important additive internal noise limits primarily reflect contributions of additive noise following nonlinearity, late in the system. This is based on data from experiments in attention in quite similar perceptual tasks. In these experiments, stimulus enhancement (additive internal noise reduction) was observed without external noise exclusion (Lu & Dosher, 1998a; Lu, Liu, & Dosher, 1999) and in others, external noise exclusion was observed without stimulus enhancement (Lu & Dosher, 1998b; Dosher & Lu, 1999). Neither observation should be possible if the additive noise sources prior to the template were contributing significantly to the limiting internal noise processes.

5.4. Relation to neural mechanisms

The visual system is often modeled in terms of an array of early channels sensitive to different spatial frequencies, and orientations, at each of many locations in retinal space (Graham, 1989). In contrast, the PTM considers the observer in terms of a whole system, input–output analysis. It is useful to expand the linking relationship between the two levels of description.

External noise exclusion in the PTM model corresponds to tuning the filter or template in such a way that more external noise is filtered or removed from the decision variable. However, template or filter tuning at the level of the whole system need not correspond to the tuning of individual filters corresponding to channels at the level of a multiple channel model. Instead, increasingly more successful external noise filtering might be accomplished by reducing the weight on the decision outputs from irrelevant channels, and increasing the weight given to those channels that are most relevant to the task. Similarly, additive internal noise reduction in the PTM model might reflect a reduction in the connection between irrelevant channels, each of which is limited by its own additive internal noise, and the final decision structure. The strengthening of con-

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[13] In fact, given the form of model utilized here noise prior to (location 2) or after (location 3) nonlinearity and multiplicative noise are completely indistinguishable. If $\gamma_1 \neq \gamma_2$ and crossproducts are included in the formulation of multiplicative noise, additive internal noise before and after nonlinearity may be distinguishable. In Lu and Dosher (1998a) required $\gamma_1 \neq \gamma_2$, and it was possible to rule out additive noise before the nonlinearity in favor of additive noise after the nonlinearity.

nections between relevant basic visual channels and the decision unit, and corresponding reduction of connection between irrelevant channels and the decision unit, are illustrated in Fig. 10.

Reweighting the connections between basic visual channels and a decision unit has the consequence of reducing contributions of external noise and also reducing additive internal noise (improving stimulus enhancement) at the level of the observer, as described by the PTM model. Whenever the inputs from irrelevant channels are reduced, *both* aspects of improvement specified by the PTM model analysis must follow: the external noise passing through an irrelevant channel and the additive internal noise in that channel are reduced simultaneously. A channel reweighting model of perceptual learning provides an explicit rationale for the mixture of filtering or exclusion of external noise and additive internal noise suppression at the level of the observer[14]. Channel reweighting predicts that external noise exclusion and stimulus enhancement (additive internal noise reduction) should co-occur (although they need not be exactly coupled). Changes in external noise exclusion with practice in the absence of changes in additive internal noise would either rule out channel reweighting as an explanation, or would imply that individual channels are free of additive internal noise.

Retuning of the template at the whole system level may naturally seem to suggest retuning of individual channels during perceptual learning. Indeed, we cannot rule out the possibility that individual channels were retuned during perceptual learning. However, the perceptual learning results can be accommodated by changes associated with channel reweighting alone. Taking the PTM model seriously, the bandwidth of the PTM filter at the end of training can be estimated (Appendix B). Spatial frequency bandwidths early in training were estimated to be on the order of almost two octaves. Final bandwidths were estimated to be on the order of one octave or less (see Appendix B for details), a value which is broadly consistent with the estimated bandwidths for a single channel (Graham, 1989). This observation is consistent with physiological observations that perceptual learning of auditory frequency may remap cortex by extending regions of active neurons tuned to a trained frequency (Kilgard & Merzenich, 1998) while not necessarily reducing the tuned bandwidth of any individual neuron (Weinberger, 1995).

Channel reweighting could be accomplished in a learning network by a method which changes the weights from each channel to a decision unit depending on its relationship to a correct decision. This idea is similar to ideas of Schiffrin and Schneider (1977), Schneider and Schiffrin (1977), who argued that improvements in performance related to automaticity essentially strengthened the connections between stimuli and responses. A similar conclusion resulted in an analysis of expertise in the identification of the sex of newborn chicks (Biederman & Shiffrar, 1987).

If perceptual learning is primarily accomplished by a reweighting of channel inputs, then perceptual learning may reflect neural plasiticity neither at the level of the basic visual mechanisms themselves, nor at the level of a general cognitive strategy or decision mechanism, but at an intermediate level of connecting basic visual mechanisms to a decision structure. We favor this speculative *linking structure postulate*: initial components of perceptual learning involve neural plasticity at the intermediate level wherein the connections between basic level visual processing channels and later decision units are modified. That is, perceptual learning initially constructs or modifies perceptual categorization structures which support perceptual decisions. This explanation has the advantage that perceptual learning of one task need not affect the performance of previously learned but similar tasks. If perceptual learning retuned basic visual mechanisms then learning one task would necessarily affect previously learned tasks. Certain perceptual learning phenomena clearly support the training of intermediate structures. For example, there is evidence from prism experiments that perceptual learning of several prism conditions establishes correction structures which can then coexist, allowing the rather rapid selection and switching between prisms (Welch, Bridgeman, Anand & Browman, 1993). Another example that argues against the direct retuning of basic channels is the ability to simultaneously learn related but different perceptual tasks (Liu & Vaina, 1998). Channel reweighting is one form of template relearning (Ahumada & Beard, 1997).

This model of perceptual learning suggests several testable extensions or developments. If the reweighting of channels includes selection of location, this would offer an explanation for the location specificity of the training. The rate of perceptual learning, and the asymptotic performance after extensive learning might depend on stability of spatial frequency and orientation of the Gabor stimuli and the stability of the training location. Further experimentation and modeling will be necessary to fully explore both the generality and specificity of the channel reweighting model and the linking structure postulate as general explanations of learning in basic perceptual tasks.

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[14] When the gain on multiplicative noise is unchanged with practice, the multiplicative noise in channels not tuned to the stimulus is a direct reflection of external noise only and is hence not distinguishable from external noise.

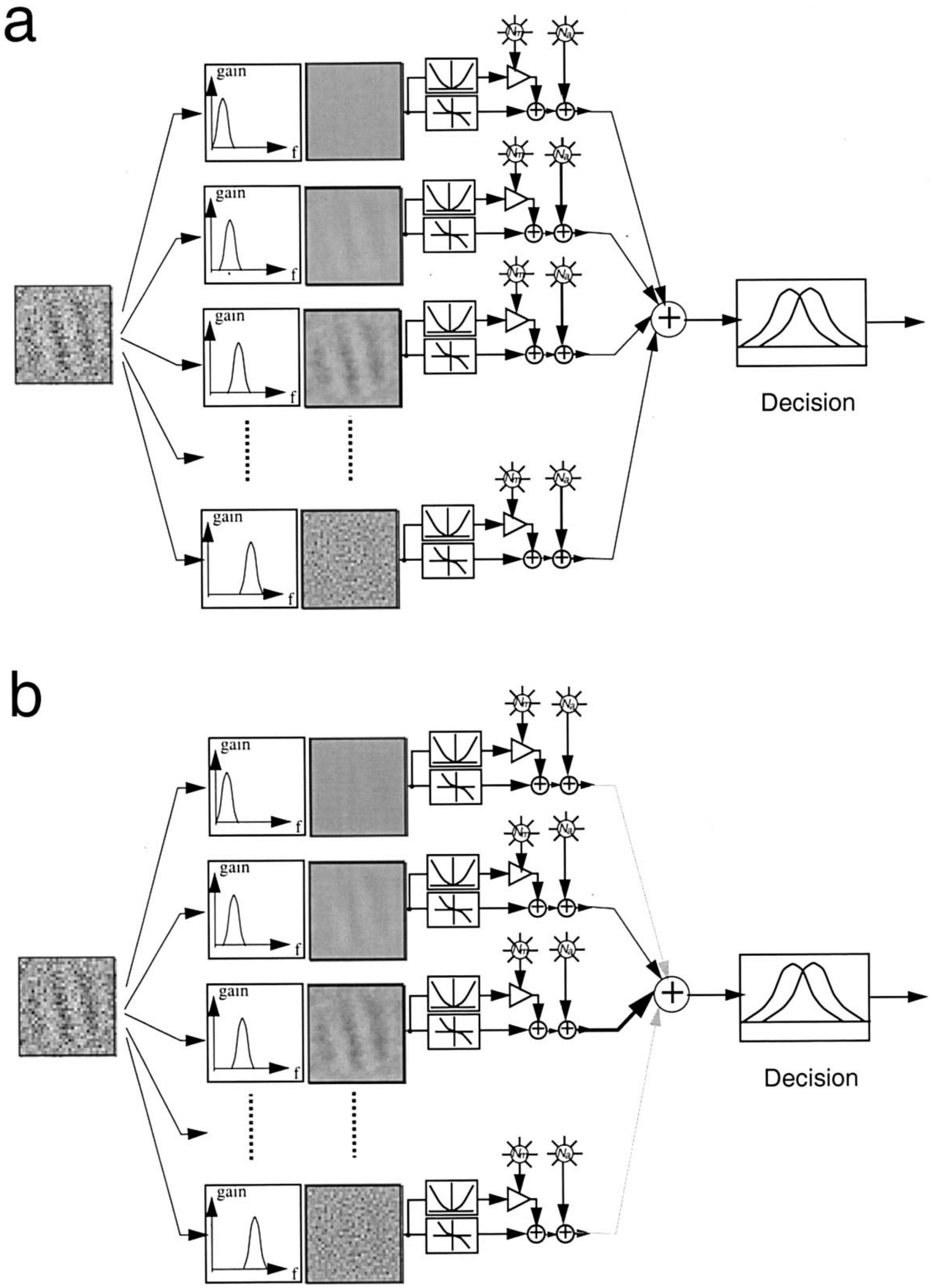

Fig. 10. Perceptual learning reweights the inputs to a decision process from basic visual channels. (a) Early in practice, the decision process weights multiple visual channels. (b) Late in practice, the decision process weights the stimulus-relevant visual channels more heavily. The signal plus noise image is shown on the left, and is subsequently processed through standard spatial frequency tuned visual channels shown schematically, to yield the filtered images shown. The image power is passed through the nonlinear transducer functions. Each visual channel is illustrated with its own internal multiplicative and additive noise sources representing processing inefficiencies. Finally, the integrated output of these visual channels is input to a decision process, illustrated at right. Channel reweighting is one possible account of perceptual learning in this task.

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Appendix A. Analysis of model variants

This appendix outlines the relationship between PTM variants with additive internal sources at three locations in the model: (1) before the template or filter; (2) after the template but before multiplicative noise; and (3) after multiplicative noise; or (4) all three. The development in Fig. 2 placed additive internal noise following multiplicative noise, location (3).

Equivalent additive internal noises quantify performance limitations which may include photon noise, sampling noise, noise in neural transmission, decision noise, and other forms of processing inefficiencies. Certain of these, such as photon noise, must occur early before the template, while other inefficiencies plausibly occur later in the processing system.

Here we demonstrate that these multiple sources of additive noise can be reparameterized as a rescaled late additive noise (3) of the form considered in this paper (see also Lu & Dosher, 1998a, 1999; Dosher & Lu, 1999). This reparameterization provides a model structure which allows reductions in internal additive noise (stimulus enhancement) and exclusion of external noise (filter or template retuning) to be separately estimated.

For this development, we consider the d' form of the essential PTM signal detection relationships for any single condition. These relationships may be expressed for multiple conditions by the addition of weighting parameters A_m, A_a, or A_f, indexed by c ondition. The key simplifying aspects of this approach involve the replacement of random variables by expectations, and the elimination of cross products in determining multiplicative noise. This was justified in the case of this experiment by the similarity of fitted models with and without crossproducts.

The signal detection relation in the PTM model considers one source of additive internal noise after multiplicative noise (3) Eq. (1):

$$d'^2 = \frac{(\beta c)^{2\gamma_1}}{A_f^2 N_{\mathrm{ext}}^{2\gamma_1} + A_m^2 N_m^2(\beta^{2\gamma_2} c^{2\gamma_2} + A_f^2 N_{\mathrm{ext}}^{2\gamma_2}) + A_a^2 N_a^2}.$$

Now consider a complex model with three internal additive noises, N_1, N_2, and N_3, as defined above, and an internal multiplicative noise N'_m (Eq. (6)):

$$d'^2 = \frac{(\beta' c)^{2\gamma'_1}}{\{A'^2_f(N_{\mathrm{ext}}^{2\gamma'_1} + N_1^{2\gamma'_1}) + A_2^2 N_2^{2\gamma'} + A'^2_m N'^2_m(\beta'^{2\gamma'_2} c^{2\gamma'_2}} \\ + A'^2_f N_{\mathrm{ext}}^{2\gamma'_2} + A'^2_f N_1^{2\gamma'_2} + A_2^2 N_2^{2\gamma'_2}) + A_3^2 N_3^2\}. \tag{6}$$

(As in Eq. (1), we chose a simplified form of multiplicative noise without crossproducts.) A. are in general further subscripted by condition, e.g. A_f (1), …

This more complex form (Eq. (6)) can be reorganized (Eq. (7)):

$$d'^2 = \frac{(\beta' c)^{2\gamma'_1}}{\{A'^2_f N_{\mathrm{ext}}^{2\gamma'_1} + A'^2_m N'^2_m + (\beta'^{2\gamma'_2} c^{2\gamma'_2} + A'^2_f N_{\mathrm{ext}}^{2\gamma'_2})} \\ + A'^2_m N'^2_m(A'^2_f N_1^{2\gamma'_2} + A_2^2 N_2^{2\gamma'_2}) + A'^2_f N_1^{2\gamma'_1} + A_2^2 N_2^{2\gamma'_1} \\ + A_3^2 N_3^2\}. \tag{7}$$

This is functionally equivalent to the original form (Eq. (1)), with (Eq. (8)):

$$A_a^2 N_a^2 = A'^2_f N_1^{2\gamma'_1} + A_2^2 N_2^{2\gamma'_1} + A'^2_m N'^2_m(A'^2_f N_1^{2\gamma'_2} + A_2^2 N_2^{2\gamma'_2}) \\ + A_3^3 N_3^2. \tag{8}$$

Functional equivalence requires the equation of coefficients of external variables, N_{ext} and c. Equivalence of the parallel (first two) forms of Eqs. (1) and (7) yield the mappings:

$$\begin{cases} \beta = \beta' \\ \gamma_1 = \gamma'_1 \\ \gamma_2 = \gamma'_2 \\ A_f(1) = A'_f(1) \equiv 1 \\ \ldots \\ A_f(K) = A'_f(K) \\ A_m(1) = A'_m(1) \equiv 1 \\ \ldots \\ A_m(K) = A'_m(K) \\ N_m = N'_m \\ A_a^2(1) N_a^2 = A'^2_f(k) N_1^{2\gamma'_1} + A_2^2(1) N_2^{2\gamma'_1} + A'^2_m(1) N'^2_m \\ (A'^2_f(1) N_1^{2\gamma'_2} + A_2^2(1) N_2^{2\gamma'_2}) + A_3^3(k) N_3^2 \\ \ldots \\ A_a^2(k) N_a^2 = A'^2_f(k) N_1^{2\gamma'_1} + A_2^2(k) N_2^{2\gamma'_1} + A'^2_m(k) N'^2_m \\ (A'^2_f(k) N_1^{2\gamma'_2} + A_2^2(k) N_2^{2\gamma'_2}) + A_3^3(k) N_3^2 \\ A_a(1) \equiv 1 \end{cases}$$

The quantity $A'^2_m N'^2_m$ in Eq. (7) serves the same function as $A_m^2 N_m^2$ in Eq. (1), and if only one condition were available A_m would be subsumed into N_m. However, our applications focus on the comparison of *at least two conditions*. In this case, one condition ($k = 1$) is always selected as a reference condition for the other $K - 1$ conditions, and $A.(k) \equiv 1$. If the parameter values for the more complex model with three noises N_1, N_2, and N_3 (right side) (Eqs. (6) and (7)) were known, the $3K + 5$ variables in the simpler model (Eq. (1))

would be solved from the $3K+5$ equations, and there exists one unique solution for the simple model parameters. On the other hand, if the parameter values for the simpler model (left side) (Eq. (1)), were known, the $5K+5$ variables in the more complex model (Eqs. (6) and (7)) are under constrained given only $3K+5$ equations, and there exist nonunique solutions. The simple model (left) is always one of these solutions.

That is, every complex model with three locations of additive noise, or any model with any one or two locations of noise, may be re-expressed in terms of a model with additive noise after multiplicative noise (N_a) Conversely, any model with additive noise after multiplicative noise can also be re-expressed as some form of model with all three noises (case 4), although there is no unique solution. The practical consequence is that it will be impossible to rule out the model where all additive noise in any system is after multiplicative noise (location 3) and it will not be possible on the basis of whole system behavior to uniquely partition additive noise into these three sources. Certain patterns of condition differences may, however, place constraints on the partition.

In general, in the current model, it is not possible to distinguish additive noise at locations (2) and (3). (They may be distinguished in certain circumstances if $\gamma_1 \neq \gamma_2$ and the model including full crossproducts in multiplicative noise were considered, but these conditions do not apply in this experiment.) Hence, it is sufficient to consider distinctions between additive noise at location (1) (early) and location (3) (late). Certain patterns of condition effects may place constraints, ranging from modest to full, on the partitioning of noise between pre- and post-template locations. These follow from the requirement that conditions differing in external noise exclusion ($A_f(i)$) require equal reductions in additive noise in location (1). Hence, a finding that condition differences are larger in high noise than in low noise constrains some additive noise, and the processing limits it represents, to be localized following the template. In the extreme case where conditions are identical in low noise (where performance is limited by additive internal noise), but differ in high noise (controlled by the perceputal filter), this rules out limiting additive noise prior to the template. This pattern has in fact been observed in several attentional paradigms in some tasks (Lu & Dosher, 1998b; Dosher & Lu, 1999).

Appendix B

Estimates of the bandwidth of spatial frequency tuning under the PTM model are developed here. These calculations are necessarily approximate.

Independent Gaussian (white) pixel noise theoretically has a uniform power spectrum over achievable frequencies from 0 to $f_{\max}$, where $f_{\max}$ is determined by the pixel grid of the display ($f_{\max} = 1/\text{minimum\_period}$, in degrees of visual angle). The total power in the noise, $N_{\text{ext}}^2 = t_{\text{ext}} \int_0^{f_{\max}} h \, \mathrm{d}f$, where h is the height of the uniform power spectrum, so $h = N_{\text{ext}}^2/(f_{\max} t_{\text{ext}})$.

The signal stimulus is a Gabor patch with center frequency f_0. We assume that the perceptual filter shape is a *scaled* Gaussian over spatial frequencies, $g(f) = \beta \mathrm{e}^{-(f-f_0)^2/2\sigma^2}$.[15] This has a gain of β at f_0, which corresponds to the PTM assumption that the perceptual filter has a gain (height) of β for a signal valued stimulus, f_0.

The PTM model chooses β (scales the filter) so that the noise power passed through the perceptual filter is set equal to N_{ext}^2, an arbitrary free scaling which avoids the necessity of carrying a cN_{ext}^2 through the PTM equations. Thus, the PTM model chooses β such that $t_{\text{ext}} \int_0^{f_{\max}} h[\beta \mathrm{e}^{-(\mathrm{f}-\mathrm{f}_0)^2/2\sigma^2}]^2 \mathrm{d}f = N_{\text{ext}}^2$. The value t_{ext} represents the temporal window over which noise frames are sampled. This can be rewritten as: $N_{\text{ext}}^2 = t_{\text{ext}} h \beta^2 \sqrt{2\pi}\sigma \int_0^{f_{\max}} 1/\sqrt{2\pi}\sigma \, \mathrm{e}^{-(f-f_0)^2/\sigma^2} \mathrm{d}f$. Assuming that $f_{\max} > f_0 + 2.5\sigma$ and $0 < f_0 - 2.5\sigma$, the integral can be approximated as 1.0. Rearranging, $\sigma = f_{\max}/\sqrt{\pi}\beta^2$.

In order to provide a numerical estimate from this formula, we must give reasonable estimates of values of $f_{\max}$, t_{ext}, and β. Our 64 × 64 pixel display subtended 1.54° × 1.54°, so $f_{\max} \approx 1/(2(1.54/64)) = 20.83$ cycle/deg. The display sequence included external noise before and after the signal frame. Finally, the average β for our observers was approximately 3.6. Using these values for $f_{\max}$ and β, the estimate of σ is 0.91 cycle/deg.

Bandwidth is calculated at half height. Since the filter is a scaled Gaussian, half height occurs at 1.2σ. At the beginning of practice ($A_s = 1.0$), the spatial frequency bandwidth of the filter is calculated at $2.3 \pm 1.2(0.91)$ cycle/deg, or 1.2–3.4 cycle/deg, for a ratio of 2.84, corresponding to between one and two octaves. The spatial frequency bandwidth is calculated in a similar way for performance at the end of training, where approximately 1/2 N_{ext} is passed through the retuned filter. This yields an estimate of σ of 0.46, corresponding to a bandwidth of 1.7–2.8, for a ratio of 1.7 or approximately one octave.

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[15] These calculations neglect the orientation tuning and focus exclusively on spatial frequency. Published estimates of the bandwidth of spatial frequency channels in early vision also ignore orientation tuning in their analyses, so this is appropriate for comparison.

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