Available online at www.sciencedirect.com
SCIENCE DIRECT®
Vision Research 46 (2006) 1996–2007
Vision Research
www.elsevier.com/locate/visres

Level and mechanisms of perceptual learning: Learning first-order luminance and second-order texture objects

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

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

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

Received 21 August 2005; received in revised form 23 November 2005

Abstract

Perceptual learning is an improvement in perceptual task performance reflecting plasticity in the perceptual system. Practice effects were studied in two object orientation tasks: a first order, luminance object task and a second-order, texture object task. Perceptual learning was small or absent in the first-order task, but consistently occurred for the second-order (texture) task, where it was limited to improvements in low external noise conditions, or stimulus enhancement [Dosher, B., & Lu, Z. -L. (1998). Perceptual learning reflects external noise filtering and internal noise reduction through channel reweighting. *Proceedings of the National Academy of Sciences of the United States of America*, *95* (23) 13988–13993; Dosher, B., & Lu, Z. -L. (1999). Mechanisms of perceptual learning. *Vision Research*, *39* (19) 3197–3221], analogous to attention effects in first- and second-order motion processing [Lu, Z. -L., Liu, C. Q., & Dosher, B. (2000). Attention mechanisms for multi-location first- and second-order motion perception. *Vision Research*, *40* (2) 173–186]. Perceptual learning affected the later, post-rectification, stages of perceptual analysis, possibly localized at V2 or above. It serves to amplify the stimulus relative to limiting internal noise for intrinsically noisy representations of second-order stimuli.

Keywords: Perceptual learning; Mechanisms of perceptual learning; Stimulus enhancement; Internal noise reduction; First-order luminance system; Second-order texture system

1. Introduction

Perceptual learning, or the improvements in performance with training or practice, is virtually ubiquitous in perceptual tasks. In this paper, we examine and contrast perceptual learning in the domains of first-order (luminance) stimuli and second-order (texture) stimuli. The task is a simple one—discriminating the orientation (right- or left-pointing) of letter objects at fovea. Perceptual learning in these tasks was assessed through measuring contrast thresholds in an external noise paradigm. A perceptual template model (PTM) of the observer distinguishes between mechanisms of perceptual learning—when it occurs—that reflect learned amplification of the stimulus and learned retuning to exclude external noise in the stimulus. Perceptual learning differs profoundly for the comparable tasks using luminance and texture stimuli, implying a higher, post-rectification, level of perceptual learning for this second-order character orientation task.

1.1. Perceptual learning

Perceptual learning has been demonstrated in a wide range of visual judgments in many different task domains, including detection or discrimination of visual gratings (DeValois, 1977; Fiorentini & Berardi, 1980, 1981; Mayer, 1983), stimulus orientation judgments (Dosher & Lu, 1998; Shiu & Pashler, 1992;Vogels & Orban, 1985), motion direction discrimination (Ball & Sekuler, 1982, 1987; Ball,

* Corresponding author. Tel.: +1 949 824 6801; fax: +1 949 824 2517.
E-mail address: bdosher@uci.edu (B.A. Dosher).

0042-6989/$ - see front matter © 2006 Published by Elsevier Ltd.
doi:10.1016/j.visres.2005.11.025

Sekuler, & Machamer, 1983), texture discrimination (Ahissar & Hochstein, 1996; Karni & Sagi, 1991, 1993), time to perceive random dot stereograms (Ramachandran & Braddick, 1973), stereoacuity (Fendick & Westheimer, 1983), hyperacuity and vernier tasks (Beard, Levi, & Reich, 1995; Bennett & Westheimer, 1991; Fahle & Edelman, 1993; Kumar & Glaser, 1993; McKee & Westheimer, 1978; Saarinen & Levi, 1995), and object recognition (Furmanski & Engel, 2000), see (Dosher & Lu, 1999b; Fine & Jacobs, 2000) for reviews.

However, the nature and magnitude of perceptual learning may depend upon the level or complexity of the task (Fine & Jacobs, 2002) and the eccentricity or noisiness of the tests (Lu & Dosher, 2004). In certain tasks and conditions, perceptual learning may not occur at all (Herzog & Fahle, 1997; Lu & Dosher, 2004). The limits of perceptual performance and the malleability of these limits with perceptual learning may be different in distinct tasks, and may reflect distinct mechanism(s) of learning. These properties, in turn, will point to the neural substraits of perceptual computations, and inform us about different classes of plasticity in each task domain. The goal is to understand the circumstances under which learned plasticity is possible and to relate these observations to known brain systems and representations. Studying perceptual learning in first- and second-order systems may inform us about the locus and system of learning in the two tasks.

1.2. First- and second-order systems

The distinction between first- and second-order systems has been important in the domains of visual motion perception (Cavanagh & Mather, 1989; Chubb & Sperling, 1989; Lu & Sperling, 1995, 2001b; Sperling, Chubb, Solomon, & Lu, 1994) and in pattern and texture perception(Chubb & Sperling, 1988; Sutter & Graham, 1995), and object perception (Regan, 2000). The first-order visual system operates directly on luminance representations while the second-order visual system operates on pre-processed (i.e., rectified) representations to which the first-order system is blind. The visual system is exquisitely sensitive to luminance patterns and to luminance inputs to motion systems, whereas second-order texture inputs to motion or pattern systems are often characterized by reduced sensitivity (Lu & Sperling, 2001b). Proposed systems for the processing of texture patterns (Regan, 2000; Sutter & Graham, 1995; Wilson, Ferrera, & Yo, 1992) share formal properties with the systems for processing second-order motion (Chubb & Sperling, 1989; Lu & Sperling, 2001a, 2001b; Solomon & Sperling, 1995). In the proposed systems, luminance stimuli are processed through a system of first-order linear filters, often characterized as a bank of spatial-frequency and temporal frequency filters typical of computations in V1 (Fig. 1A). Processing of second-order texture stimuli is generally modeled as a second pathway with a “sandwich” process in which a point-wise non-linearity such as rectification (or half-rectification and pooling,

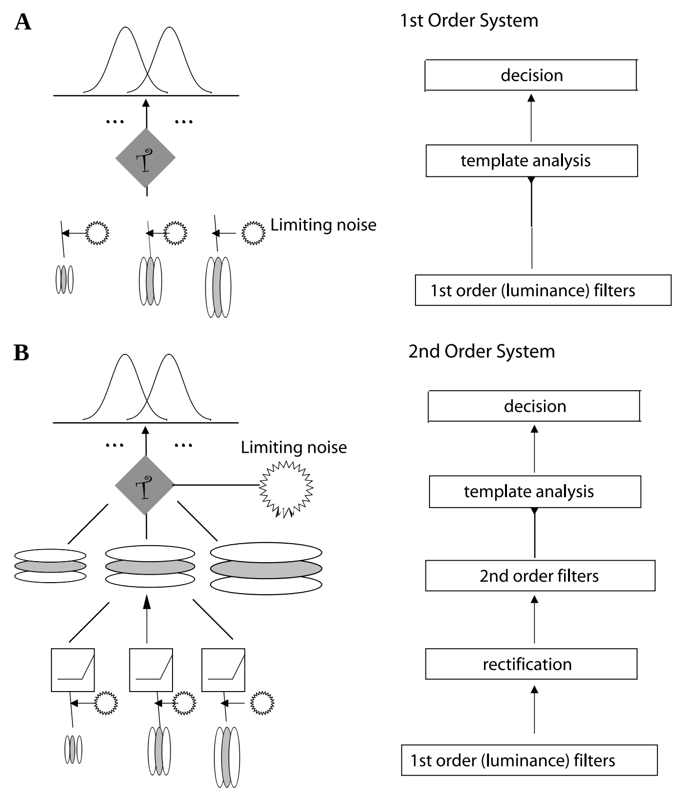

Fig. 1. A schematic two-level architecture for analysis of second-order task processing. First-order tasks could be based on an initial Fourier channels, consistent with analysis at V1, while second-order tasks are based on rectified representations, consistent with analysis at V2 or higher.

segregating and then combining positive and negative) is carried out between the initial processing by linear filters and subsequent linear filtering (Fig. 1B). This second stage of the pathway has been associated with computations at V2 or above (Lin & Wilson, 1996), where cells selectively responsive to texture or orientation boundaries, but not carrier elements have been reported (von der Heydt, Peterhas, & Baumgartner, 1984), but see (Chaudhuri & Albright, 1977). The second-order (non-Fourier) pathways exhibit characteristically higher (1.4–3×) discrimination thresholds and require longer presentation durations (Lin & Wilson, 1996). Within this framework, perceptual learning may take place at different stages of the processing system reflected in first-order and second-order stimuli and tasks.

Comparing perceptual learning in analogous first- and second-order letter orientation tasks will have implications for the localization of the learning in the first- and second-order systems. Moreover, if perceptual learning occurs for either task, the mechanism of the learning (stimulus enhancement or external noise exclusion, see Section 1.4) can be identified through external noise studies. Learning in the second-order task in the absence of learning in the comparable first-order task would suggest that perceptual learning occurs in the second (post-rectification) stages of the non-Fourier pathways, at the level of V2 or above. If perceptual learning occurs in both tasks, but the identified mechanisms are different, then this would imply learning in different pathways or at different levels for the two forms of stimuli, or an order of perceptual learning in the two systems.

1.3. Comparing perceptual learning in first- and second-order tasks

Several observations, mostly in the motion domain, suggest that learning may differ between first-order and second-order pattern tasks. For example, asymmetries in transfer of perceptual learning between a first-order and a second-order motion task suggests the engagement of distinct perceptual learning processes (Zanker, 1999). An analogy between perceptual learning and attention (e.g., Dosher & Lu, 2000)—both of which reflect a change of state of the observer and demonstrate analogous performance patterns—also suggests different properties of first- and second-order stimuli. There are significant attention limitations in the simultaneous processing of two or more patches of second-order motion stimuli (Dosher, Landy, & Sperling, 1989), where these same limitations do not occur for first-order motion stimuli. Judgments of second-order motion are strongly influenced by attention, while judgments of first-order motion may be affected little or not at all by attention (Lu, Liu, & Dosher, 2000) (but see (Allen & Ledgeway, 2003)). Furthermore, this attention effect on the perception of second-order motion stimuli has the unusual property of being restricted to clear (low external noise) situations (see PTM section below for an interpretation). Taken together, these observations may lead to the prediction that perceptual tasks based on second-order texture stimuli may also be more susceptible to perceptual learning, and that the mechanisms of that learning may parallel the mechanisms of attention. The patterns of perceptual learning for closely controlled first- and second-order tasks will provide important information about the locus and independence of perceptual learning.

1.4. Perceptual learning and the perceptual template model

The perceptual template model (PTM) characterizes the limitations of perceptual processes in an observer. The PTM and systematic external noise tests were developed to identify the mechanism(s) of change of state of the observer due to attention or perceptual learning (Dosher & Lu, 1998, 1999a; Lu & Dosher, 1998). A brief quantitative description of the model appears in Appendix A. If perceptual learning occurs either in a first-order task or in a second-order task, then the mechanism of that learning can be identified through the PTM and external noise tests. In studying perceptual learning, the performance of the observer is measured as a joint function of training or practice and the amount of white Gaussian external noise added to the signal stimuli. Three mechanisms of perceptual learning can be distinguished: (1) *stimulus enhancement* reduces absolute thresholds by amplifying the input stimulus, including both the signal and the external noise, relative to internal (additive) noise. It is signified by performance improvements only in low or zero external noise conditions but not in high external noise conditions. (2) *Perceptual template retuning* optimizes the perceptual template to exclude external noise or distractors. Its signature is performance improvements restricted to high external noise conditions. And (3) *contrast-gain control or multiplicative noise reduction* improves the contrast saturation properties of the perceptual system. It is associated with improvements throughout the full range of external noise, with the magnitude of the improvements differing with the criterion accuracy. Performance threshold measures at multiple criterion levels (e.g., 70% and 80% correct) provide sufficient constraints to distinguish these mechanisms and various mixtures of them (Dosher & Lu, 1999b; Lu & Dosher, 1999).

The external noise plus perceptual learning paradigm has been used in a number of studies to characterize improvements of the perceptual system during the course of perceptual learning (Chung, Levi, & Tjian, 2005; Dosher & Lu, 1998, 1999b, 2005; Gold, Bennett, & Sekuler, 1999; Lu & Dosher, 2004; Saarinen & Levi, 1995; Tjian, Chung, & Levi, 2002). Perceptual learning of peripheral Gabor orientation identification (Dosher & Lu, 1998, 1999a), as well as the identification of faces or filtered noise patterns from a small set of alternatives (Gold et al., 1999) all showed improved performance (reduced contrast thresholds) across all external noise conditions reflecting simultaneous improvements in external noise exclusion (template retuning) and stimulus enhancement (stimulus amplification),[1] although the improvements in performance due to the two mechanisms may be decoupled in magnitude (Dosher & Lu, 2005).

Recently, a case of pure external noise exclusion was documented for Gabor orientation identification (about 45°) at fovea (Lu & Dosher, 2004). In this case, performance in zero or low external noise never improved despite extensive practice, while performance in high external noise improved systematically with practice. It was also reported briefly that there was no perceptual learning for orientation discriminations (±8°) about the vertical—even in high external noise. Orientation judgments for luminance (first-order) objects tested at fovea might exhibit the same pattern of perceptual learning in high noise, suggesting that perceptual learning might or might not occur for letter orientation (left or right facing) for first-order stimuli at fovea. In contrast, based on the impact of spatial attention cueing on second-order motion perception only in low external noise, it is possible that orientation judgments for texture

[1] An equal magnitude of (log) improvement at all performance criteria (e.g., 65%, 75%, and 85%) identifies these results as a mixture of stimulus enhancement and external noise exclusion and not a change in contrast gain control or multiplicative noise properties (Dosher & Lu, 1998, 1999b).

(second-order) objects tested at fovea might instead reflect improvements with perceptual learning in stimulus enhancement. The following experiments evaluate perceptual learning in luminance (first-order) and texture (second-order) object orientation identification tasks.

2. General methods

2.1. Observers

Eight observers participated in the study, four in each Experiment. Observers had normal, or corrected to normal, vision and were naïve to the purpose of the experiment.

2.2. Apparatus

The experiments were conducted on a Macintosh 7300 computer, using PsychToolbox (Brainard, 1997; Pelli, 1997) subroutines and Matlab programs (Mathworks, 1998). The stimuli were displayed on a Nanao Technology Flexscan 6600 monitor with a P4 phosphor at a 480×640 pixel spatial resolution and a refresh rate of 120 Hz. A special circuit (Pelli and Zhang, 1991) combined two eight-bit outputs of the internal Macintosh graphics card to produce 12.6 bits, or 6144 distinct gray levels. A psychophysical procedure was used to generate a lookup table that linearly translated pixel gray-levels into display luminance (Li, Lu, Xu, Jin, & Zhou, 2003). The minimum, maximum, and neutral luminance (l_0) values were 1, 50, and 25 cd/m^2, respectively.

2.3. Design

The perceptual task consisted of discriminating the orientation (forward or mirror-reversed) of the letter K represented either using luminance contrast (Experiment 1) or through texture contrast (Experiment 2) combined with one of eight levels of external noise. The eight external noise conditions ranged from no external noise to high external noise (see Stimuli, Fig. 2). The texture contrast or luminance necessary to achieve one of two criterion threshold accuracy levels in each external noise condition was measured using adaptive staircase methods (Levitt, 1971). Criterion accuracies of 70.7% and 79.3%, corresponding to d's of 1.089 and 1.634, were estimated with 2/1 and 3/1 staircases that reduced the contrast by 10% ($C_{n+1} = 0.9\ C_n$) after two or three correct responses and increased the contrast by 10% ($C_{n+1} = 1.1\ C_n$) after each error. The sixteen staircases—8 noise conditions × 2 staircases—were interleaved within each 1008-trial session (72 for each 3/1 staircase and 54 for each 2/1 staircase). Observers practiced either the luminance task (Experiment 1) or the texture task (Experiment 2) for five sessions (days). In Experiment 2b, observers practiced the luminance task for five sessions after training on the texture task. The final value of the staircases on 1 day served as starting values for the next.

2.4. Stimuli

The luminance or texture letter was centered within a 64×64-pixel grid, with a 'stroke width' of 6 pixels. The luminance-defined characters took on a luminance value darker than the background while texture-defined characters were filled with a 2×2 checkerboard texture (see Fig. 2). The luminance of the luminance letter ($l_{\min}-l_0$, expressed as a percent of the maximum range) or the contrast ($l_{\max\ \text{or}\ \min} - l_0$, as a percent of the maximum range) of the texture letter was determined by adaptive staircase methods tracking either 70.7% correct or 79.3% correct. Each 64×64-pixel noise image consisted of random Gaussian pixel noise image had contrasts drawn from a Gaussian distribution with mean 0 and standard deviation $N_{\text{ext}} \in \{0, 0.02, 0.04, 0.08, 0.12, 0.16, 0.25, 0.33\}$ relative to the neutral luminance, windowed within a circular region with radius of 32 pixels. The maximum value of 0.33 for the highest noise provides a range for $\pm 3\sigma$ of the Gaussian within a full luminance range of $[-1, +1]$ relative to the neutral luminance. External noise frames and the letter were combined via temporal integration, N-S-N.

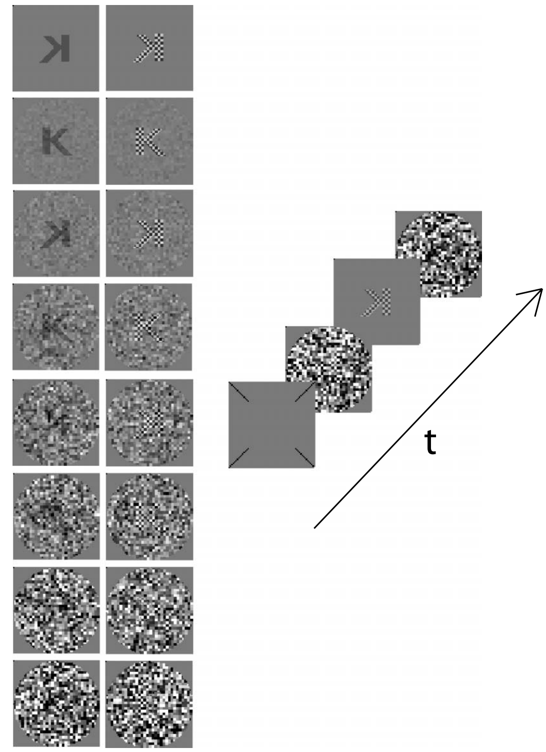

Fig. 2. Illustration of texture (checkerboard) and luminance (dark gray) stimuli embedded in eight levels of external noise (left) and of a trial display sequence (right). Signal and external noise stimuli were combined via temporal integration (16.7 ms each of N-S-N).

2.5. Procedure

A key press initiated each session. Each trial began with a fixation display for 150 ms, followed by a noise (or blank) image, a signal character image, and another noise (or blank) image, each presented for 16.67 ms, followed by a blank screen until response. The observer pressed the "j" key on the keyboard for a right-facing character and "f" key on the keyboard for a left-facing (reversed) character. The observer was allowed to take several breaks between trials; these breaks were brief or the observer often elected to continue immediately.

3. Experiment 1 results

3.1. Contrast threshold versus external noise practice functions

Perceptual learning should reduce thresholds with practice. The slopes of the $\log_2$ contrast thresholds as a function of days of practice index learning, where negative slopes reflect threshold improvements. The slopes of $\log_2$ thresholds, averaged over staircases and observers, as a function of days of practice were statistically indistinguishable from 0 (no learning) individually for all eight external noise levels. There was a slight trend (with mixed significance) towards *increased* thresholds with practice for observers GB and JJ,[2] no consistent trend for observer MH, and slight and variable decreases for RC in the individual observer regression analyses. These analyses clearly did not show a consistent trend towards perceptual learning for the first-order task. Any changes in threshold with practice were as likely to reflect slight deterioration with practice as improvement.

3.2. Perceptual template model

The perceptual template model (PTM) was used to characterize the impact of external noise level on thresholds and estimate learning, if it occurs. The regression tests and flat thresholds as a function of days indicated an absence of consistent systematic learning in these data. Consistent with the regression analyses, a PTM model analysis showed no consistent systematic *improvements* in performance over days of practice in these luminance-object data for three of the four observers. As with the regression slope analysis, observers GB and JJ showed some tendency to deterioration of performance, observer MH differed relatively little over days, and observer RC showed some tendency to improvement in low external noise. The average threshold versus external noise contrast (TVC) functions are shown in Fig. 3 along with smooth curves representing the fit of the perceptual template model (PTM) with no learning over days. The PTM model has four parameters that set the overall level of performance and also how much higher the 3/1 thresholds are than the 2/1 thresholds (a proxy for the slope of the psychometric function): N_{add}, additive internal noise that determines the thresholds in low external noise, N_{mult}, multiplicative internal noise that increases with the contrast of the stimulus to produce Weber-law behavior, β, the gain on the target stimulus in the perceptual template, and γ the transduction non-linearity in the system. For the average data, these values were: $N_{add}, = 0.02$, $N_{mult}, = 0.05$, $\beta = 0.90$, and $\gamma = 1.60$. These values are representative.

3.3. Summary

Over the time range of this study, there was no consistent improvement in luminance-object (first-order) orientation judgments. While we cannot absolutely rule out changes in performance (negative as well as positive), there is no consistent perceptual learning. This finding adds to observations in the literature where training simple, low-level tasks at fovea may result in little or no perceptual learning in clear displays (Dorais & Sagi, 1997; Fiorentini & Berardi, 1981; Furmanski & Engel, 2000; Lu & Dosher, 2004; Matthews, Liu, Geesaman, & Qian, 1999; Ramachandran & Braddick, 1973). In contrast to several other examples, no learning is exhibited for this task in high noise displays either. While there is no compelling explanation as to why certain tasks are not susceptible of improvement (at least over this time scale), perceptual training studies documenting failures to learn are more likely for foveal tasks. Equivalent tasks carried out in the periphery generally will exhibit perceptual learning improvements. Perhaps the fovea is already optimized for these luminance letter stimuli[3].

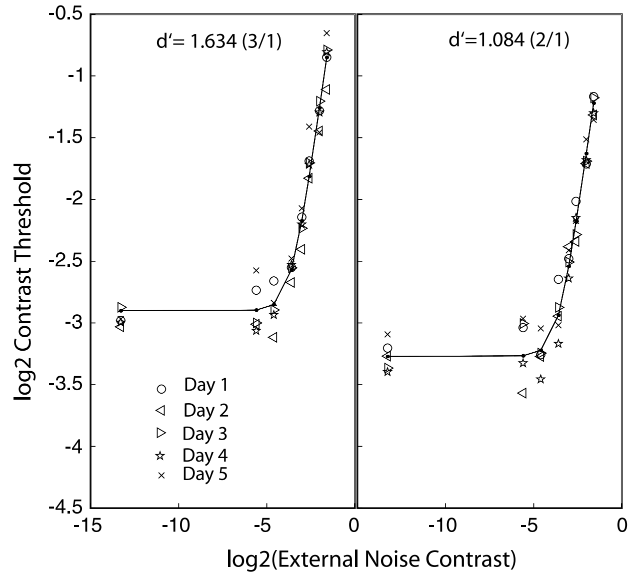

Fig. 3. Average threshold versus contrast (TVC) data for luminance task of Experiment 1 with the PTM model (see text) shown as the smooth curve. Data are shown for two criteria (3/1 and 2/1 staircases).

4. Experiment 2 results

4.1. Contrast threshold versus external noise contrast and practice

The $\log_2$ contrast thresholds, averaged over staircases and observers, were analyzed as a function of session (day) of practice separately for each external noise level. Regression analyses show performance improvements with practice for this second-order texture object orientation task, with steeper improvements in low external noise levels. The average slope of $\log_2$ thresholds as a function of

[2] Indeed, two observers in the luminance character experiment participated for additional days of practice, and unexpectedly performance deteriorated—in some cases dramatically. It is unclear whether this reflected a real and paradoxical effect of practice in this case, or issues with motivation in a situation in which learning typically does not occur.

[3] One reviewer suggested that the lack of perceptual learning for this first-order task might reflect the fact that the size of the stimuli was well above the first-order acuity limit. However, based on the equivalence of letter identification over a wide range of viewing distances (Parish & Sperling, 1991) and based on the observed transfer of learning over scales (Lu & Dosher, 2004), the current results are likely to hold over a wide range of letter sizes.

day (consistent with an exponential improvement in performance with practice) ranged from −0.14 in the lowest external noise to −0.04 in the highest external noise level (first four slopes, $p < .05$; next four slopes, ns, for each external noise condition considered separately).

So, there is significant, consistent learning in the second-order texture task. The larger learning effect in low noise suggests that stimulus enhancement (gain amplification) is the mechanism of perceptual learning. A quantitative analysis of the mechanism evaluates the threshold versus external noise contrast (TVC) functions. The $\log_2$ contrast thresholds for the average data (Fig. 4) are shown as a function of contrast of external noise (TVC) at each of the two criterion accuracy levels (3/1 and 2/1 staircases, left and right, respectively). The curves of individual observers were very similar (see Appendix B). The smooth curves correspond to the fits of the perceptual template model (see below). The solid lines correspond to the first day (heavy solid line) and the fifth day (lighter solid line) of practice, which differ predominantly in low external noise; training has little or no effect on performance in high external noise.

4.2. Perceptual template model

The mechanism of perceptual learning was evaluated using perceptual template models (PTM) with improvements in external noise exclusion or filtering only, stimulus enhancement only, both, or neither. The best-fitting model, as determined through nested significance tests, is shown as smooth curves in Fig. 4. All four observers showed significant perceptual learning through stimulus enhancement but no significant change in external noise exclusion. The best-fitting model (Table 1) assumes that improvements are restricted to stimulus enhancement, showing improvements in low external noise. This model did not differ significantly from a "Full" model with perceptual learning improving both stimulus enhancement and external noise exclusion (all nested-F tests with $p > .10$ except JP $p > .05$, see Table 1). The stimulus enhancement model provides a significantly improved fit relative to a model with no improvement due to learning (all nested-F tests with $p < .001$). In this best-fitting model, perceptual learning is captured in improved relative stimulus enhancement, which is equivalent to a (relative) reduction in internal additive noise, A_a, for each practice day. The first day is set at 1, $A_a(1) \equiv 1.0$. Improvements due to practice take the form of a reduction in additive noise ($N_a(\mathrm{k}) = A_a(\mathrm{k})$ N_{add}, $A_a \leqslant 1.0$). For the average data, the values of the four parameters of the basic PTM were: $N_{\mathrm{add}}, = 0.07$, $N_{\mathrm{mult}}, = 0.08$, $\beta = 0.53$, and $\gamma = 1.40$. These values are representative of those for the individuals. For the average data, the ratio of last day to first day ($\mathrm{A}_a(5)/\mathrm{A}_a(1)$) is 0.624; the ratios for individual observers are 0.558, 0.468, 0.400, and 0.805. The pattern of improvements for intermediate days is somewhat variable for each observer, but show general improvements over intermediate days.

In summary, perceptual learning operates on texture objects primarily through learned improvements in stimulus enhancement and does not substantially alter task performance in high external noise—at least when the texture pattern of the objects overlaps with the spectral properties of the external noise. The observer has learned to "upweight" the stimulus. The implications of this finding both for perceptual learning of second-order stimuli and more generally for the perceptual template framework are considered in Section 5.

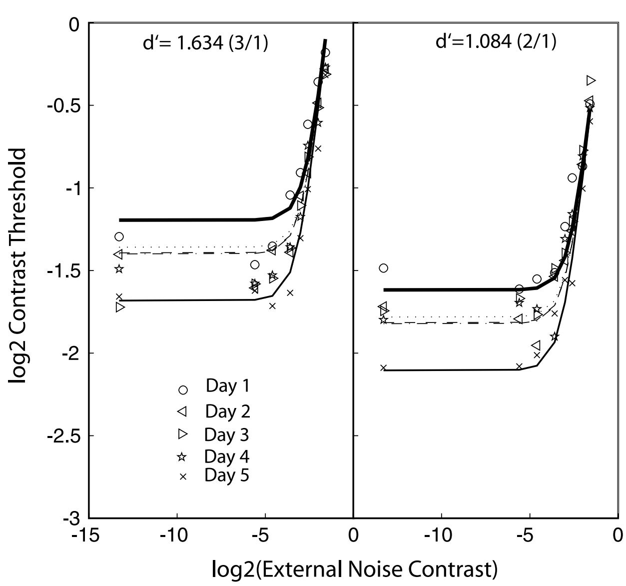

Fig. 4. Contrast thresholds, averaged over observers, as a function of external noise contrast (TVC functions) for five practice days in the texture (second-order) letter task. Data are shown for two criteria (3/1 and 2/1 staircases). The dark heavy lines are Day 1, and the lighter heavy lines are Day 5. Smooth curves are the fit of a PTM model with perceptual learning through stimulus enhancement (see Table 1 for parameter values).

4.3. Practice of luminance stimuli following texture practice

Following practice on the texture object orientation task, the same observers performed the luminance object task for five sessions. The regression slopes of $\log_2$ contrast thresholds, averaged over staircases and observers as a function of day of practice did not differ significantly from 0 for any of the eight external noise levels (range from −0.03 to 0, each $p > 0.15$). Although there is day-to-day variation in performance (especially in low noise conditions), and perhaps a hint of bias towards negative slopes (performance improvements), there were no statistically reliable improvements in performance, consistent with Experiment 1.The results of the analysis with the perceptual template model (PTM) were consistent with a "null," or no-practice effect, since the fit of this model did not significantly reduce the quality of the fit relative to a "full" model with all possible practice effects. Two observers, JD and YC, did show some marginal variation in thresholds in low external noise, but these appeared to be daily fluctuations not systematic improvements in performance. We show the average threshold (TVC) data in Fig. 5. Although a

Table 1
PTM parameters Experiment 2

Observers					
Parameters	JD	JP	VC	YC	AV
N_a	0.05	0.05	0.05	0.07	0.07
N_m	0.03	0.03	0.08	0.06	0.08
β	0.46	0.55	0.49	0.49	0.53
γ	1.83	1.80	1.68	1.46	1.40
$A_a(2)$	0.77	0.61	0.58	1.00	0.85
$A_a(3)$	1.00	0.64	0.55	0.85	0.83
$A_a(4)$	0.92	0.57	0.55	0.92	0.82
$A_a(5)$	0.56	0.47	0.40	0.81	0.62
r^2	0.897	0.907	0.801	0.843	0.930
$F_{\text{Full vs. NO-SE}}$ ($df = 8, 64$)	3.5132^{***}	4.3429^{****}	6.1206^{****}	5.1575^{****}	3.5079^{***}
$F_{\text{SE vs. NULL}}$ ($df = 4, 72$)	9.114^{****}	7.9698^{****}	14.6002^{****}	11.5502^{****}	10.5852^{****}
$F_{\text{Full vs. NO-NE}}$ ($df = 8, 64$)	1.3122^{ns}	$2.0789^{\#}$	1.2622^{ns}	0.3006^{ns}	0.8833^{ns}

*** $p < .001$.
**** $p < .0001$.
$^{\#}$ $p < .10$.

result of no perceptual learning for these first-order stimuli might, by itself, have reflected complete transfer of learning from the texture to the luminance objects, the consistency with the results of Experiment 1 suggest instead that the luminance (first-order) system does not consistently exhibit learning. Prior optimization of performance through second-order task practice did not trigger subsequent improvements with practice in the first-order task.

4.4. Comparisons of thresholds for the texture and luminance task

The thresholds for second-order tasks are typically higher than for the comparable first-order task. Lin and Wilson (Lin & Wilson, 1996) computed indices of 1.3–2.5 times higher second-order thresholds in a variety of task comparisons. In this case, we chose to compare the average thresholds of the last two days of practice on the texture task and the first 2 days of practice on the following luminance task in the same individuals. The thresholds reflect the threshold difference from neutral luminance in both cases. The ratio of second-order to first-order log thresholds in the average data was 1.8, and the ratios were 2.8, 1.8, 1.2, and 2.9, respectively, for observers JD, JP, VC, and YC. (VC has relatively high thresholds in both tasks.) These are compatible with higher estimates of β, or gain, of the perceptual template for the signal stimulus for luminance than for texture objects: The β's for the luminance objects were 1.14, 0.98, 0.63, and 0.98 for the four observers, and 0.85 for the average data; the corresponding values were 0.46, 0.55, 0.49, 0.49, and 0.53 for the texture objects, or an average ratio of 1.83 to 1, or almost two to one, compatible with the empirical ratios, as well as those cited by Lin and Wilson (Lin & Wilson, 1996). Interestingly, the second-order elevation ratios are higher in low external noise (average about 2.5) and lower in high external noise (average about 1.7). This observation merits further investigation[4].

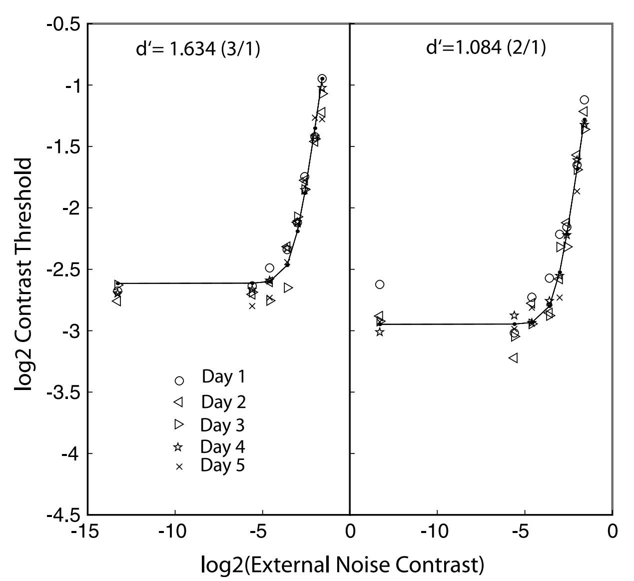

Fig. 5. Average threshold versus contrast (TVC) data for luminance task of Experiment 2b with best-fitting, no learning, PTM model shown as the smooth curve.

4.5. Summary

Practice on texture object orientation judgments resulted in a systematic improvement in performance in low

[4] Although the monitor was linearized, the human perceptual systems may introduce first-order "contamination" due to asymmetries in the perception of physically equal dark and light deviations from mean luminance. Even if this contamination were as high as 15% (Lu & Sperling, 2001a, 2001b), the first-order information would only be at about 27% of threshold, suggesting a very small impact in the second-order task.

external noise conditions, corresponding to improvements in stimulus enhancement due to perceptual learning. The thresholds of the texture task are elevated by an average factor of 1.8 compared to the luminance task, consistent with prior reports for other kinds of judgments (e.g., Lin & Wilson, 1996). Subsequent practice with luminance object orientation judgments did not result in systematic performance improvements. This appears to reflect a fundamental difference in the sensitivity to practice for texture (second-order) stimuli and luminance (first-order) stimuli. This result parallels that spatial attention effects for second-order motion stimuli (Lu, Liu, & Dosher, 2000).

5. General discussion

5.1. Summary

Two experiments, yielding three data sets, investigated the ability for observers to learn and improve their perceptual performance in first-order and in second-order object (letter) orientation judgments. Surprisingly, (regular/mirror) orientation judgments for first-order letters at fovea were not consistently susceptible of improvement—whether in low or in high levels of external noise. In a previous study, oblique Gabor orientation judgments at fovea showed no learning in low external noise, but did show significant learning in high external noise (Lu & Dosher, 2004) for orientation judgments around 45°. They also showed no learning in either low or high noise for orientation judgments about the vertical. In the current study, there was no consistent evidence for perceptual learning for first-order stimuli, whether they were trained initially, or following training on second-order stimuli. It does not appear that further training would have guaranteed learning, since several observers who trained with first-order stimuli for additional sessions, if anything, showed worsening performance. It is possible that this lack of learning reflects the pre-existing knowledge of letter characters at fovea. Significant learning did occur for orientation judgments of letters defined by a second-order texture pattern, where performance improvements predominantly occurred in low external noise conditions.

The pattern of learning in these experiments has a strong and direct analogy to the effects of attention on motion direction discrimination (left or right) judgments: attention had little or no effect on first-order motion judgments, but resulted in significant improvements in low external noise on second-order motion judgments (Lu et al., 2000). (It is of course possible that either learning or attention may impact both first-order motion or first-order orientation judgments under certain circumstances (Allen & Ledgeway, 2003).) The importance of attention and of perceptual learning for second-order stimuli suggests an influential role for stimulus amplification, corresponding to stimulus enhancement in the PTM, for these stimuli. Further research should evaluate the claim that stimulus enhancement is characteristically associated with state-change related performance improvements in second-order stimuli. In the current experiment, the grain of the texture that defines the letter is relatively similar to the grain of the external noise. Filtering out other sections of the broad spectrum of external noise should still be of value, however, this may already be reasonably optimized even without practice in fovea (i.e., Dosher, Liu, Blair, & Lu, 2004).

5.2. When learning fails

The observations of weak or no consistent learning in the task of first-order letter object orientation discrimination adds to the list of tasks in the literature for which little or no learning has been reported (Dorais & Sagi, 1997; Fiorentini & Berardi, 1981; Furmanski & Engel, 2000; Lu & Dosher, 2004; Matthews et al., 1999; Ramachandran & Braddick, 1973). It appears that many of these cases are simple, low level tasks displayed at fovea without external noise. Based on our prior findings for orientation discrimination about the vertical (Lu & Dosher, 2004) we thought it possible that perceptual learning might not occur, or if it did, learning would occur in high external noise, reflecting learned external noise exclusion. We have no firm understanding of why we do not find the same pattern in the current letter-orientation task as in the earlier oblique Gabor orientation task. Some cases of failures of learning (Herzog & Fahle, 1997; Rubin, Nakayama, & Shapley, 1997) occur for extremely fine discriminations where initial performance is below normal threshold accuracy levels (60%), but this is not the case here: the two orientations differ clearly, and the staircase procedures keep performance levels near 80%. We can only speculate that the lack of capacity for substantial learning may reflect the over-learned status of letters. The result points out, however, the lack in the field at large of a firm predictive analysis of when perceptual learning occurs and when it does not.

5.3. Level of perceptual learning

The pattern of little or no learning in the luminance letter (first-order) task, combined with successful learning in the texture letter task, is consistent with a locus of learning at the second, post-rectification, level of the second-order pathway. This learning may be based on representations at the level of V2 or higher (Fig. 2B). Although V1 neurons can respond to second-order or texture stimuli (e.g., Chaudhuri & Albright, 1977), it is likely that important second-order processing occurs between V2 and V4 (Baker & Mareschal, 2001; Landy & Graham, 2004; Lennie, 1998). The analysis of Baker (Baker & Mareschal, 2001) is that the second stage filters in second-order "...processing could be any of the quasi-linear neurons of early visual cortical areas, though the low preferred spatial frequencies in our data suggest a greater contribution from second tier areas (A18, V2)" (p. 15). Landy and Graham (2004) suggest that, although V1 cells may exhibit some simpler non-linearity, it is unlikely that V1 is the substrait of such functions as texture and region segregation, and that "these functions probably occur in V2 through V4..."

The output of early linear filters, corresponding to first-order processing, is rectified, and then subjected to analysis by larger scale linear templates or filters in the second-order stages. This process is limited by internal noise at both stages, as well as by any external noise (Sperling, 1989). Given the reductions in precision reported for most second-order tasks (Lin & Wilson, 1996; Lu & Sperling, 1999), it appears that significant *internal* limiting noise must occur associated with the latter stage of processing. Stimulus enhancement (relative stimulus amplification) overcomes this internal limiting noise.

We propose that perceptual learning for the texture-defined letters takes place late in the second-order pathway. If instead we had observed, for example, parallel patterns of learning in the first-order and second-order tasks, we might have concluded that the locus (or at least one major locus) of improvement was in the first-order layer. Stimulus enhancement might occur through re-weighting or strengthening of the connections from the first layer of analysis to the second layer of the "sandwich," or from the second-order filters to the template, resulting in a useful relative amplification of the stimulus in relation to internal noise sources (Fig. 6). It is reasonable to assume that the rectified channels may not naturally have strong connection to the higher-order object templates or filters, reflecting the fact that we do not normally read checkerboard letters. Re-weighting, or "upweighting," of the connections between early sensory representations and later decision analysis is consistent with our recent proposals of perceptual learning through multi-channel re-weighting (Dosher & Lu, 1998; Dosher & Lu, 1999b; Petrov, Dosher, & Lu, 2005a; Petrov, Dosher, & Lu, 2005b).

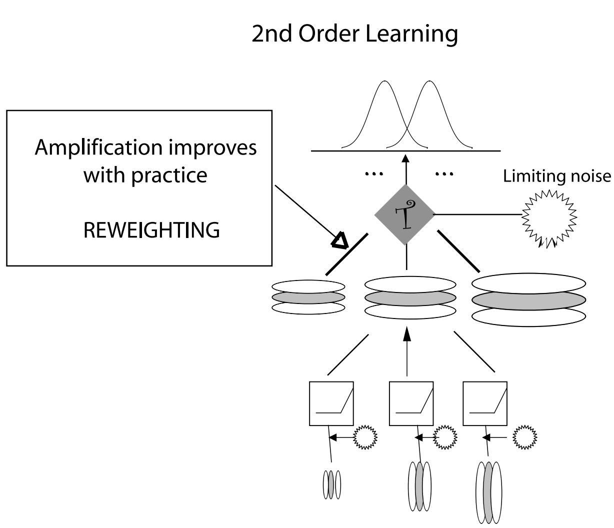

Fig. 6. A schematic two-level architecture for second-order task processing and perceptual learning. Learning occurs at the second-order stage, after rectification, through reweighting of the first-order inputs.

Acknowledgments

This research was supported by NSF Grants BCS-9911801 and BCS-9910678, and NIMH Grant 1 R01 MH61834-01.

Appendix A

The Perceptual Template Model (Lu & Dosher, 1999) quantitatively models human performance in signal detection and discrimination. In the PTM, perceptual inefficiencies are attributed to three limitations: internal additive noise that is associated with absolute thresholds in perceptual tasks; perceptual templates that is often tuned to a range of stimulus features and often allows unnecessary influence of external noise or distractors on performance; and internal multiplicative noise that is associated with Weber's Law behavior of the perceptual system. The basic PTM consists of four parameters in the basic PTM (Lu & Dosher, 1998): gain to the signal stimulus (β), exponent of the non-linear transducer function (γ), internal additive noise (N_{add}), and coefficient of the multiplicative internal noise (N_{mul}). The three mechanisms of perceptual learning were implemented by multiplying the corresponding noise[5] in the PTM with learning parameters $A_{\mathrm{add}}(t)$, $A_{\mathrm{ext}}(t)$, and $A_{\mathrm{mul}}(t)$ in each training block t, with $A_{\mathrm{add}}(1) = A_{\mathrm{ext}}(1) = A_{\mathrm{mul}}(1) = 1.0$ (Dosher & Lu, 1998; Dosher & Lu, 1999b, Lu & Dosher, 2004). In the most saturated PTM with all three mechanisms of perceptual learning, thresholds are expressed as functions of external noise by in the following equation:

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

All eight possible versions of PTM models, consisting of various combinations of the three mechanisms of perceptual learning, were fit to each set of TvC functions, separated by training and transfer sessions. A least-square minimization procedure based on *fmins* in Matlab 6.5 (Mathworks, 1998) was used to search for the best-fitting parameters for each PTM: (1) $\log(c^{\mathrm{theory}})$ was calculated from the model using an initial set of parameters for each external noise condition, performance criterion, and training block; (2) Least-square L was calculated by summing the squared differences $sqdiff = [\log(c^{\mathrm{theory}}) - \log(c)]^2$ across all the conditions; (3) Model parameters were adjusted by *fmins* to

[5] In the PTM, stimulus enhancement is mathematically equivalent to internal additive noise reduction Lu and Dosher (1998).

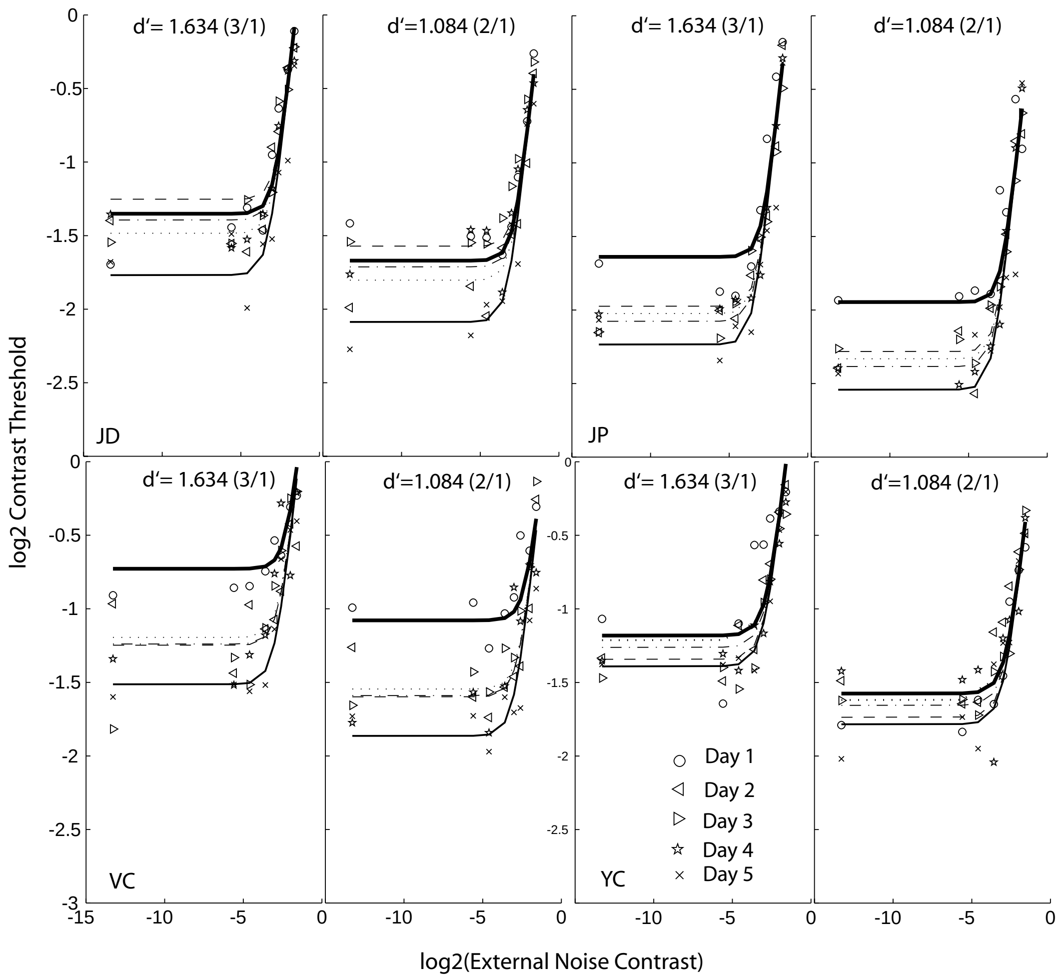

Fig. 7. Contrast thresholds for individual observers as a function of external noise contrast (TVC functions) for five practice days in the texture (second-order) letter task. Data are shown for two criteria (3/1 and 2/1 staircases). The dark heavy lines are Day 1, and the lighter heavy lines are Day 5. Smooth curves are the fit of a PTM model with perceptual learning through stimulus enhancement (see Table 1 for parameter values).

search for the minimum L using gradient descend and re-iterating steps (1) and (2). The proportion of variance accounted for by the model form was calculated using the r^2 statistic

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

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

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

$$F(\mathrm{d}f_1, \mathrm{d}f_2) = \frac{(f^2_{\text{full}} - r^2_{\text{reduced}})/\mathrm{d}f_1}{(1 - r^2_{\text{full}})/\mathrm{d}f_2}, \quad \text{(A3)}$$

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

Appendix B

See Fig. 7.

References

Ahissar, M., & Hochstein, S. (1996). Learning pop-out detection: Specificities to stimulus characteristics. *Vision Research, 36*(21), 3487–3500.

Allen, H. A., & Ledgeway, T. (2003). Attentional modulation of threshold sensitivity to first-order motion and second-order motion patterns. *Vision Research, 43*(27), 2927–2936.

Baker, C. L., & Mareschal, I. (2001). Processing of second-order stimuli in the visual cortex. In C. Casanova, & M. Ptito (Eds.), *Progress in Brain Research, 134* (pp. 12:11-21): Elsevier Science B.V.

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

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

Ball, K., Sekuler, R., & Machamer, J. (1983). Detection and identification of moving targets. *Vision Research, 23*(3), 229–238.

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

Bennett, R. G., & Westheimer, G. (1991). The effect of training on visual alignment discrimination and grating resolution. *Perception & Psychophysics, 49*(6), 541–546.

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

Cavanagh, P., & Mather, G. (1989). Motion: The long and short of it. *Spatial Vision, 4*, 103–129.

Chaudhuri, A., & Albright, T. D. (1977). Neuronal responses to edges defined by luminance vs. temporal texture in macaque area V1. *Visual Neuroscience, 14*, 949–962.

Chubb, C., & Sperling, G. (1988). Drift-balanced random stimuli: A general basis for studying non-Fourier motion perception. *Journal of the Optical Society of America A, 5*(11), 1986–2007.

Chubb, C., & Sperling, G. (1989). Two motion perception mechanisms revealed through distance-driven reversal of apparent motion. *Proceedings of the National Academy of Sciences of the United States of America, 86*, 2985–2989.

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

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

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

Dosher, B., Liu, S.-H., Blair, N., & Lu, Z.-L. (2004). Attention and the patial window of the perceptual template. *Vision Research, 44*, 1257–1271.

Dosher, B., & Lu, Z.-L. (1998). Perceptual learning reflects external noise filtering and internal noise reduction through channel reweighting. *Proceedings of the National Academy of Sciences of the United States of America, 95*(23), 13988–13993.

Dosher, B., & Lu, Z.-L. (1999a). Attention to a validly cued location improves performance by excluding external noise. *Investigative Ophthalmology & Visual Science, 40*(4), S797.

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

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

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

Dosher, B. A., Landy, M. S., & Sperling, G. (1989). Kinetic depth effect and optic flow: I. 3D shape from Fourier motion. *Vision Research, 29*(12), 1789–1813.

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

Fendick, M., & Westheimer, G. (1983). Effects of practice and the separation of test targets on foveal and peripheral stereoacuity. *Vision Research, 23*(2), 145–150.

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

Fine, I., & Jacobs, R. A. (2002). Comparing perceptual learning across tasks: A review. *Journal of Vision, 2*, 190–203.

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

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

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

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

Herzog, M. H., & Fahle, M. (1997). The role of feedback in learning a vernier discrimination task. *Vision Research, 37*(15), 2133–2141.

Karni, A., & Sagi, D. (1991). Where practice makes perfect in texture-discrimination—Evidence for primary visual-cortex plasticity. *Proceedings of the National Academy of Sciences of the United States of America, 88*(11), 4966–4970.

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

Kumar, T., & Glaser, D. A. (1993). Initial performance, learning and observer variability for hyperacuity tasks. *Vision Research, 33*(15), 2287–2300.

Landy, M. S., & Graham, N. V. (2004). Visual perception of texture. In L. M. Chalupa & J. S. Werner (Eds.), *The visual neurosciences* (pp. 1106–1118). Cambridge, MA: MIT Press.

Lennie, P. (1998). Single units and cortical organization. *Perception, 27*, 889–935.

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

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

Lin, L.-M., & Wilson, H. R. (1996). Fourier and non-fourier pattern discrimination compared. *Vision Research, 36*(13), 1907–1918.

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

Lu, Z.-L., & Dosher, B. (1999). Characterizing human perceptual inefficiencies with equivalent internal noise. *Journal of the Optical Society of America A Special Issue: Noise in Imaging Systems and Human Vision, 16*(3), 764–778.

Lu, Z.-L., & Dosher, B. (2004). Perceptual learning retunes the perceptual template in foveal orientation identification. *Journal of Vision, 4*(1), 44–56.

Lu, Z.-L., Liu, C. Q., & Dosher, B. (2000). Attention mechanisms for multi-location first- and second-order motion perception. *Vision Research, 40*(2), 173–186.

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

Lu, Z.-L., & Sperling, G. (2001a). Sensitive calibration and measurement procedures based on the amplification principle in motion perception. *Vision Research, 41*(18), 2355–2374.

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

Lu, Z. L., & Sperling, G. (1999). The amplification principle in motion perception. *Investigative Ophthalmology & Visual Science, 40*(4), S199.

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

Matthews, N., Liu, Z., Geesaman, B. J., & Qian, N. (1999). Perceptual learning on orientation and direction discrimination. *Vision Research, 39*(22), 3692–3701.

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

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

Parish, D. H., & Sperling, G. (1991). Object spatial frequencies, retinal spatial frequencies, noise, and the efficiency of letter discrimination. *Vision Research, 31*(7–8), 1399–1415.

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

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

Petrov, A., Dosher, B., & Lu, Z.-L. (2005a). Perceptual learning without feedback in non-stationary contexts: Data and model. *Vision Research*, manuscript in preparation.

Petrove, A. A., Dosher, B. A., & Lu, Z.-L. (2005b). The dynamics of perceptual learning: An incremental reweighting model. *Psychological Review, 112*(4), 715–743.

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

Regan, D. (2000). *Human perception of objects: Early visual processing of spatial form defined by luminance, color, texture, motion, and binocular disparity*. Sunderland, Massachusetts: Sinauer Associates, p. 577.

Rubin, N., Nakayama, K., & Shapley, R. (1997). Abrupt learning and retinal size specificity in illusory-contour perception. *Current Biology, 7*(7), 461–467.

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

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

Solomon, J. A., & Sperling, G. (1995). 1st- and 2nd-order motion and texture resolution in central and peripheral vision. *Vision Research, 35*(1), 59–64.

Sperling, G. (1989). Three stages and two systems of visual processing. *Spatial Vision, 4*(2-3), 183–207.

Sperling, G., Chubb, C., Solomon, J. A., & Lu, Z.-L. (1994). Full-wave and half-wave processes in second-order motion and texture. In G. R. Bock, J. A. Goode, & F. Ciba (Eds.), *Higher-order processing in the visual system* (pp. 287–308). New York, NY: Wiley.

Sutter, A., & Graham, N. (1995). Investigating simple and complex mechanisms in texture segregation using the speed âccuracy tradeoff method. *Vision Research, 35*(20), 2825–2843.

Tjian, B. S., Chung, S., & Levi, D. M. (2002). Limitation of ideal-observer analysis in understanding perceptual learning. In *Twenty-seventh annual interdisciplinary conference*. Wyoming: Jackson Hole.

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

von der Heydt, R., Peterhas, E., & Baumgartner, G. (1984). Illusory contours and cortical neuron responses. *Science, 224*, 1260–1262.

Wilson, H. R., Ferrera, V. P., & Yo, C. (1992). A psychophysically motivated model for two-dimensional motion perception. *Visual Neuroscience, 9*(1), 79–97.

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