

Perceptual learning of Gabor orientation identification in visual periphery: Complete inter-ocular transfer of learning mechanisms

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Received 6 August 2004; received in revised form 8 March 2005

Abstract

We combined the external noise paradigm, the Perceptual Template Model approach, and transfer tests to investigate the mechanisms and eye-specificity of perceptual learning of Gabor orientation in visual periphery. Coupled with a fixation task, discriminating a 5 from an S in a rapid small character string at fixation, contrast thresholds were estimated for each of eight external noise levels at two performance criteria using 3/1 and 2/1 staircases. Perceptual learning in one eye was measured over 10 practice sessions, followed by five sessions of practice in the new eye to assess transfer. We found that monocular learning improved performance (reduced contrast thresholds) with virtually equal magnitude across a wide range of external noise levels with no significant change in central task performance. Based on measurements of learning effects at two performance criterion levels, we identified a mixture of stimulus enhancement and external noise exclusion as the mechanism of perceptual learning underlying the observed improvements. Perceptual learning in the trained eye generalized completely to the untrained eye. We related the transfer patterns to known physiology and psychophysics on orientation direction coding.

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Keywords: Specificity of perceptual learning; Inter-ocular transfer; Mechanisms of perceptual learning; External noise exclusion; Template returning; Stimulus enhancement; Internal noise reduction; Contrast-gain control reduction

1. Introduction

The pattern of specificity or transfer of perceptual learning between the trained and untrained eyes may implicate the physiological level at which learning takes place. Because it is widely believed there are no monocular cells in any visual cortical areas other than V1 (Hubel, Wiesel, & Stryker, 1977), eye specific perceptual learning would suggest learning sites in or below the pri-

mary visual cortex; perceptual learning that generalizes across eyes would point to learning sites in or after certain layers of the primary visual cortex. Some authors (Sagi & Tanne, 1994) have also suggested that the degree of eye-specificity of perceptual learning might be related to the involvement of multiple systems in learning a particular task: an on-line, fast (few hundred trials), binocular high-level system that improves links between high-level task-dependent units and sensory units, and an off-line, slow (days), monocular low-level system that establishes new associations and dissociations in primary sensory areas that requires consolidation for hours after stimulus presentation.

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Eye-specificity of perceptual learning have been evaluated in luminance contrast detection (Sowden, Rose, & Davies, 2002), vernier tasks (Beard, Levi, & Reich, 1995; Fahle, Edelman, & Poggio, 1995), orientation discrimination (Schoups, Vogels, & Orban, 1995), phase discrimination (Fiorentini & Berardi, 1981), pop out (Ahissar & Hochstein, 1996; Karni & Sagi, 1991; Schoups & Orban, 1996), visual search (Sireteanu & Rettenbach, 2000), and in motion perception (Ball & Sekuler, 1982, 1987; De Luca & Fahle, 1999; Lu, Chu, Doshier, & Lee, 2005). Complete or nearly complete specificity to the eye of training has been documented in luminance contrast detection (Sowden et al., 2002) [Experiment 2], hyper-acuity tasks (Fahle, 1994; Fahle et al., 1995; Poggio, Fahle, & Edelman, 1992), and texture discrimination (Karni & Sagi, 1991). Complete or nearly complete generalization from the trained to the untrained eye has been reported in luminance contrast detection (Sowden et al., 2002) [Experiment 1] and masking (Dorais & Sagi, 1997), hyper-acuity tasks (Beard et al., 1995), orientation discrimination (Schoups et al., 1995), phase discrimination (Fiorentini & Berardi, 1981), texture discrimination (Schoups & Orban, 1996), pop out (Ahissar & Hochstein, 1996), visual search (Sireteanu & Rettenbach, 1995; Sireteanu & Rettenbach, 2000), and motion direction discrimination (Ball & Sekuler, 1982, 1987; De Luca & Fahle, 1999; Griffiths & Chubb, 1995; Vaina, Sundaeswaran, & Harris, 1995). In this study, we evaluated eye-specificity of perceptual learning of Gabor orientation identification.

Neurophysiology evidence suggests that the degree of single-eye dominance and orientation selectivity of neurons in upper layers of the primary visual cortex are negatively correlated (Livingstone & Hubel, 1984; Blasdel, 1992)—mostly monocular and non-oriented cells are found in layers 4A and 4Cb (Blasdel & Fitzpatrick, 1984; Tootell, Hamilton, Silverman, & Switkes, 1988) and mostly binocular and oriented cells are found outside 4Cb (Blasdel & Fitzpatrick, 1984; Hawken & Parker, 1984; Livingstone & Hubel, 1984). Even though most neurons with orientation tuning are binocular, it is still conceivable that re-weighting of the non-oriented input to these orientation selective units could also improve performance. Such re-weighting could be monocular.

A previous study on perceptual learning of orientation discrimination (Schoups et al., 1995) using noisy stimuli found that learning largely transferred from the trained to the untrained eyes. Recently, Doshier and Lu (1998, 1999) concluded that perceptual learning of Gabor orientation identification reflected joint effects of two learning mechanisms: a template retuning mechanism that is effective in stimulus embedded in high external noise, and a stimulus enhancement mechanism that improves performance in clear or low external noise displays. Whereas the pattern of eye-specificity or transfer may depend critically on the particular task being learned, another very

important factor that has not been extensively investigated is that different strategies and/or mechanisms may be involved in learning a particular task (Doshier & Lu, 1998, 1997); and these different mechanisms may have different transfer properties (Lu et al., 2005). Joint patterns of transfer and learning mechanisms may provide significant structural constraints on inferred locus of particular mechanisms of learning.

In this study, we combined eye transfer tests with external noise manipulation and the Perceptual Template Model (PTM) to investigate the eye-specificity of mechanisms of perceptual learning in Gabor orientation identification in the visual periphery.

The external noise manipulation and the PTM observer model (Fig. 1a) were developed to study the perceptual mechanisms underlying a range of higher order functions such as attention or learning (Doshier & Lu, 1998, 1999; Lu & Doshier, 1998, 1999). In studying perceptual learning, observer performance (threshold) is measured as a joint function of training or practice and the amount of white Gaussian external noise added to the signal stimuli (“threshold versus external noise contrast or TvC functions”). Mechanisms of perceptual learning are characterized as changes of the magnitude of various observer inefficiencies. 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 (Fig. 1b). (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 (Fig. 1c). 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 (Fig. 1d). 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 (Doshier & Lu, 1999; Lu & Doshier, 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, & Tjan, 2001; Doshier & Lu, 1998, 1999; Gold, Bennett, & Sekuler, 1999; Li, Levi, & Klein, 2003; Lu et al., 2005; Lu & Doshier, 2004; Saarinen & Levi, 1995; Tjan, Chung, & Levi, 2002).

Previous studies (Doshier & Lu, 1998, 1999) on perceptual learning of peripheral Gabor orientation identification task found that perceptual learning decreased contrast thresholds virtually uniformly across external noise conditions with equal magnitude independent of the performance criterion level tested. The performance

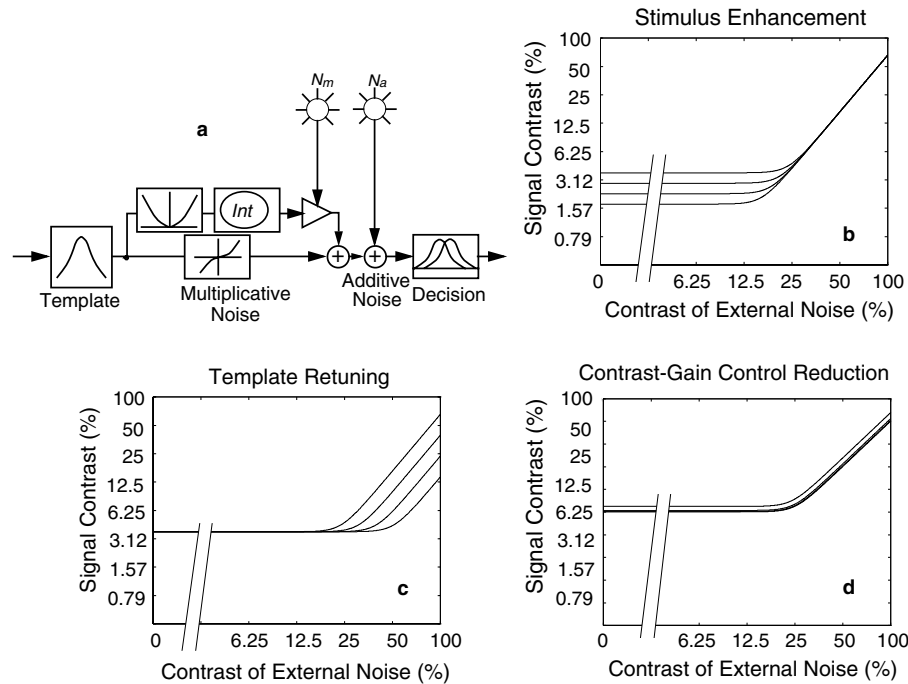


Fig. 1. (a) Perceptual template model. (b–d) Performance signatures of the three mechanisms of perceptual learning.

improvements reflected joint effects of template retuning at the level of the whole observer coupled with stimulus enhancement as the mechanisms of perceptual learning. Perceptual learning based on a mixture of mechanisms was ideally suited for the purpose of the current study, which was to investigate which perceptual learning mechanism is specific to the eye of training.

2. Methods

2.1. Observers

Three students from the University of Southern California, DJ, SL and WC, all with normal vision and naïve to the purpose of the experiment, participated in the study.

2.2. Apparatus

Matlab programs based on a version of Psychtoolbox (Brainard, 1997; Pelli, 1997) were used to conduct all the experiments on a Macintosh Power PC 7500 computer. 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 & Zhang, 1991) combined two eight-bit outputs of the internal Macintosh graphics card to produce a 12.6 bit, 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).

Observers viewed the displays with natural pupils at a viewing distance of 80 cm in a dimly lit room. The monitor display was divided into left and right halves, each containing a $8.0^\circ \times 6.4^\circ$ box, demarcated with black lines and positioned at the same height in the two halves (Fig. 2). Both boxes contained a fixation cross in the center and a $1.54^\circ \times 1.54^\circ$ stimulus window at the corresponding corners. A stereoscope rendered the left and right displays to the left and right eyes and aligned the boxes and fixation crosses. Stimuli were only shown to one eye; gray background (27 cd/m^2) was shown to the other eye. The observers were instructed to maintain fixation throughout the experiment. A chinrest was used to help observers maintain their head positions.

2.3. Stimuli

The “signals” in the perceptual learning task were Gabor patterns tilted $\pm 12^\circ$ (or $\pm \frac{\pi}{15}$) from the vertical

$$I(x,y) = I_0 \left\{ 1.0 + c \sin[2\pi f(x \cos(\pi/15) \pm y \sin(\pi/15))] \exp\left(-\frac{x^2 + y^2}{2\sigma^2}\right) \right\}, \quad (1)$$

where background luminance $I_0 = 27 \text{ cd/m}^2$, Gabor center frequency $f = 2.32 \text{ c/deg}$, Gabor spatial window $\sigma = 0.40^\circ$. The peak contrast c was set by the adaptive staircase procedures.

The Gabors were rendered on a 50×50 pixel grid, extending $1.54^\circ \times 1.54^\circ$ of visual angle. During training sessions, the stimuli were shown in the right eye and displaced to the lower right quadrant, its center displaced

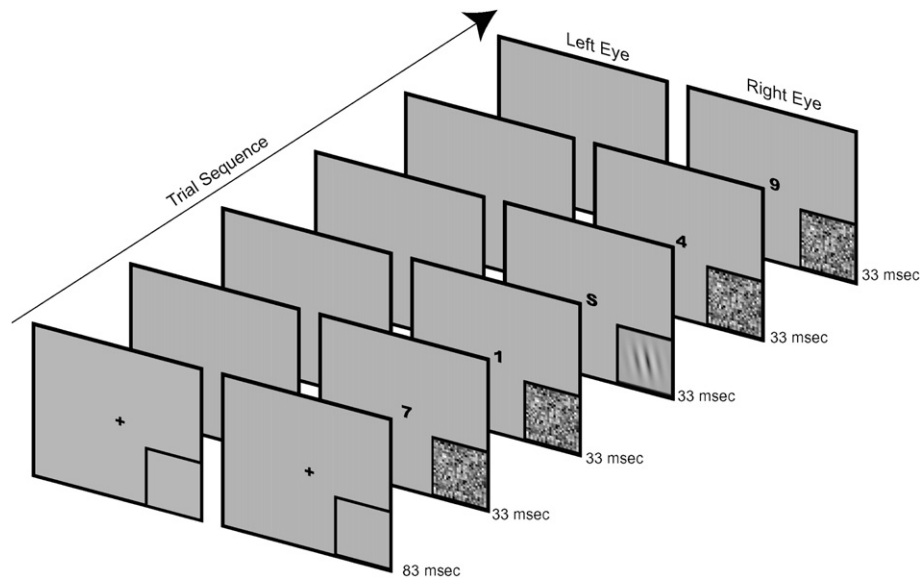


Fig. 2. Illustration of a stimulus display sequence (Experiment 1) in training sessions. All the stimuli were presented to the right eye. In transfer sessions, the stimuli were all presented to the left eye. Signal and external noise stimuli were combined via temporal integration.

from the fixation by 2.4° vertically and 3.3° horizontally. In subsequent transfer tests, the stimuli were presented in the left eye in the corresponding location (Fig. 2).

External noise images ($1.54^\circ \times 1.54^\circ$) were constructed from $0.06 \times 0.06^\circ$ pixel patches with identically distributed contrasts drawn independently from Gaussian distributions with mean 0 and standard deviation $N_{\text{ext}} \in \{0, 0.02, 0.04, 0.08, 0.12, 0.16, 0.25, 0.33\}$. Because the display contrast ranges from -1 to 1 , a sample with the maximum standard deviation of 0.33 conforms reasonably well to a Gaussian distribution. External noise and signal Gabors were combined via temporal integration.

The central task consisted of alphanumeric characters (Times font) subtending approximately $0.12^\circ \times 0.25^\circ$ of visual angle.

2.4. Design

Observers performed two tasks. The central task, identifying “S” or “5” embedded in a temporal character string, was used to ensure that observers maintained fixation.¹ Observer’s threshold contrasts at two perfor-

mance criterion levels were estimated for Gabor orientation identification at each of eight external noise levels using two inter-leaved staircase procedures (Levitt, 1971). The staircases increased signal contrast by 10% ($c_{\text{new}} = 1.10 \times c$) after every incorrect response, and decreased signal contrast by 10% ($c_{\text{new}} = 0.90 \times c$) after every three (3-down 1-up) or two (2-down 1-up) consecutive correct responses. The two staircases estimated thresholds at 79.3% and 70.7% correct, corresponding to d 's of 1.634 and 1.089 in two alternative forced-choice identification. The experimental conditions were inter-mixed. The last few trials of each staircase in a session were used to initiate the corresponding staircase in the next session.

Observers ran 10 training sessions in one eye and then five transfer sessions in the other eye. The “extra” transfer sessions were included to assess transfer as well as subsequent learning. During training sessions, all the signal/noise stimuli occurred in one eye. Stimuli were presented to the other eye for test of transfer. There were 1440 trials per session, 100 and 80 trials per 3/1 and 2/1 staircases, respectively. Each session lasted about one hour. All in all, each observer ran 21,600 trials.

2.5. Procedure

In the beginning of each session, observers adjusted the stereoscope to align the left and right eye displays. Following a key press, each trial started with a 500 ms fixation display. At the center of the display, the fixation cross was replaced by a string of five characters, each lasting 33.3 ms. The third character in the string was either a “5” or an “S”; the other characters were selected from the set {“0”, “1”, “2”, “3”, “4”, “6”, “7”, “8”, “9”}

¹ A central RSVP task is widely used in perceptual learning paradigms (Karni & Sagi, 1991; Karni & Sagi, 1993). The paradigm with identical stimulus parameters was used in Doshier and Lu (1998, 1999), who showed that perceptual learning of orientation identification in visual periphery was largely specific to the retina location. The observed retina specificity indicates that learning in this task is not due to eye fixation changes. In addition, Juttner (2001) suggests that small eye fixation changes are not important in perceptual learning tasks like ours: He found that the magnitude of perceptual learning of Gabor pattern discrimination was the same in fovea and in 3° eccentricity using very similar stimulus parameters.

without replacement. Simultaneous with the onset of the character string, a sequence of five frames, consisting of two external noise, one Gabor, and another two external noise images, appeared in the stimulus quadrant, each lasting 33.3 ms. The onset of the Gabor coincided with that of the third character at the center of the display. Both the central and peripheral stimuli occurred in only one eye. The fixation display followed stimulus presentation and lasted until the end of the trial. Observers were required to make two responses: First, identify the character in the central task; and then identify the orientation of the Gabor. An auditory beep followed each correct response. Observers were easily able to associate the feedback to the relevant response.

3. Results

3.1. Central task performance

Observers performed the central fixation task, discriminating an “S” from a “5”, at essentially constant accuracies across all training and transfer sessions: $60.9 \pm 5.7\%$, $79.9 \pm 6.8\%$ and $84.7 \pm 2.6\%$ for observers DJ, SL and WC, respectively. The external noise level in the perceptual task did not affect accuracy on the central task, based on a within subject analysis of variance using training session as the random factor ($F(7, 98) = 0.270, 0.729$ and 0.413 for DJ, SL and WC, respectively, with $p > 0.50$ for all observers).

A 2×2 contingency table classified all the trials for each observer according to response accuracies in both central and peripheral tasks. Contingency analyses on these tables found significant positive dependencies between the two tasks ($\chi^2(1) = 33.32, 20.54$ and 39.18 , for DJ, SL and WC, with $p < 0.001$ for all observers). The positive correlation suggests that the observers turned to be correct on both the central and the peripheral tasks. There were no statistically significant trade-offs between the two tasks.

A central RSVP task is known to require fixation to perform (Reeves & Sperling, 1986). The rate of letter presentation (30 letters/s) in the current study is much higher than that used in Reeves and Sperling (4.6 letters/s). The observers could not have performed the central task if they moved their fixation toward the Gabor in the periphery: a trade-off between the two tasks would have been observed. The positive correlation between the performances of the two tasks ruled out changes of eye fixation as an explanation of the observed perceptual learning effects in this study.

3.2. Learning curves

The psychophysical staircase procedure typically produced about 20 reversals (where the sign of the contrast

increment/decrement reverses) per staircase in each experimental session. Average contrast at the reversals was calculated, after excluding the first three or four reversals, depending on whether an odd or even numbers of reversals were obtained, to yield an estimate of threshold contrast. To verify that the estimated thresholds converged at the specified performance levels (70.7% and 79.3%), we pooled the data from the two staircases in each external noise condition and fitted psychometric functions to them using a maximum likelihood procedure (Lu & Doshier, 2004). Thresholds estimated from this procedure agreed very well with those calculated from the staircases ($r^2 = 0.987$).

Average learning curves—threshold as a function of training session—in training and transfer sessions were calculated for each external noise condition by averaging threshold contrasts across observers and performance criteria in each day of training. To estimate power-law learning parameters (Anderson & Fincham, 1994; Logan, 1988), the log–log learning curves were fit with linear regression functions (SPSS, 1999):

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

The learning curves are plotted in separate panels for training and transfer in Fig. 3. Training reduced thresholds in all external noise conditions ($p < 0.001$; Table 1), with an average of $49.0 \pm 5.8\%$ total reduction over 10 sessions and a rate (B) of -0.308 ± 0.064 log units reduction per log unit of training session (Eq. (2)). Learning in one eye transferred entirely to the untrained eye: Averaged across external noise levels, the threshold ratio between the first session of transfer and the last session of training is 1.000 ± 0.064 , suggesting that the thresholds in the un-trained eye were identical to those in the other, trained eye. Performance deteriorated slightly during transfer sessions: the threshold ratio between the last session of transfer and the last session of training is 1.102 ± 0.052 . The learning curves during the transfer phase of the experiment are essentially flat—none of the slopes was significantly different from 0 (Table 1). On average, threshold increased at a rate of 0.054 ± 0.023 per log unit per log session. The performance deterioration during transfer sessions, although not statistically significant, may reflect fluctuations associated with the fatigue of the perceptual system, which might have become more apparent in the absence of performance improvements.

3.3. TvC functions and PTM modeling

Observers identified the orientation of a Gabor embedded in eight levels of external noise, first in one eye during 10 sessions of training and then in the other eye during five sessions of transfer. Thresholds at two criterion performance levels ($P_c = 70.7\%$ and $P_c = 79.3\%$) were estimated in each external noise condition

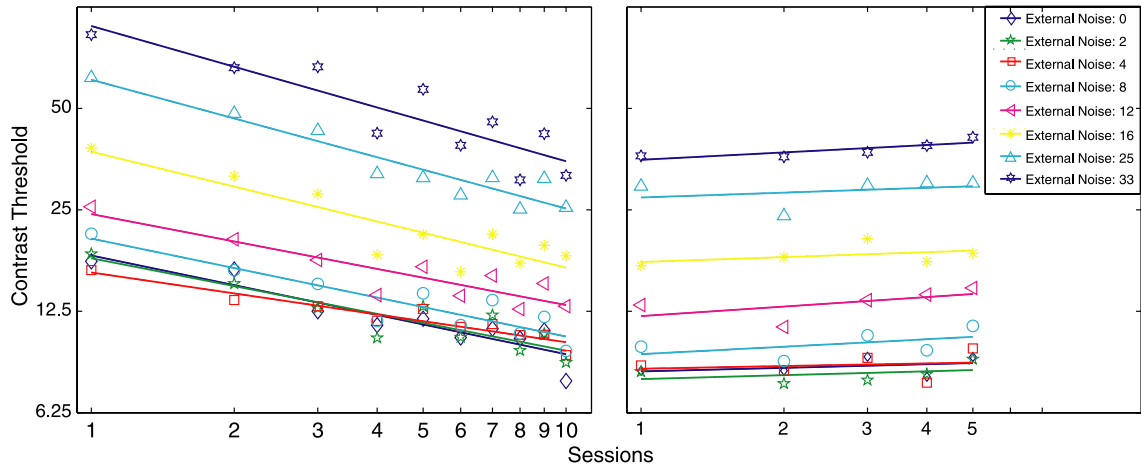


Fig. 3. Learning curves for the training (left panel) and transfer (right panel) sessions.

Table 1
Regression coefficients

N_{ext}	Training			Transfer		
	$B \pm SD$	$R \pm SD$	Sig.	$B \pm SD$	$R \pm SD$	Sig.
0.00	-0.29 ± 0.05	-2.45 ± 0.11	0.000	0.04 ± 0.05	-2.59 ± 0.08	0.545
0.02	-0.27 ± 0.05	-2.48 ± 0.11	0.000	0.04 ± 0.05	-2.67 ± 0.09	0.531
0.04	-0.21 ± 0.02	-2.62 ± 0.06	0.000	0.03 ± 0.08	-2.57 ± 0.13	0.761
0.08	-0.29 ± 0.05	-2.28 ± 0.11	0.000	0.07 ± 0.07	-2.42 ± 0.12	0.388
0.12	-0.27 ± 0.05	-2.04 ± 0.11	0.000	0.09 ± 0.08	-2.05 ± 0.12	0.300
0.16	-0.34 ± 0.06	-1.43 ± 0.15	0.000	0.05 ± 0.06	-1.51 ± 0.09	0.465
0.25	-0.38 ± 0.04	-0.72 ± 0.11	0.000	0.05 ± 0.08	-0.88 ± 0.13	0.603
0.33	-0.40 ± 0.07	-0.19 ± 0.18	0.001	0.07 ± 0.03	-0.51 ± 0.05	0.080

using adaptive staircase procedures. This design yielded a total of thirty [15 sessions \times 2 criterion levels] TvC functions, each sampled at eight external noise levels. The TvC functions for the three observers and their average are shown in Fig. 4, pooled over every two training sessions (left panels) and displayed for each single transfer session (right panels).

In the trained eye, thresholds increased fourfold as external noise increased, from about 0.121 to 0.503, averaged across the 10 training sessions. As expected, the more stringent performance criterion (79.3%) required higher thresholds than the less stringent performance criterion (70.7%). The threshold ratio between the two criterion levels is essentially constant across the eight noise levels and training sessions (mean = 1.25; SD = 0.16). Similar results were obtained in the untrained eye during transfer tests. Thresholds increased fourfold as external noise increased, from about 0.086 to 0.378 averaged across the five transfer sessions. The threshold ratio between the 79.3% and 70.7% correct performance criterion levels is also essentially constant across the eight noise levels and training sessions (mean = 1.27; SD = 0.14). Ratio constancy across external noise and practice levels indicates that practice did

not alter contrast-gain control properties of the perceptual system (Doshier & Lu, 1999; Lu & Doshier, 1999).

TvC functions over training days were fit with the PTM to identify mechanisms of learning during training and mechanisms of subsequent learning during transfer (Appendix A). Data from the two eyes were fit separately. In the trained eye, performance improved via a mixture of two mechanisms, stimulus enhancement and external noise reduction—the PTM with these two mechanisms accounted for 99.1% of the variance with 78.8% internal additive noise reduction (or an equivalent 372% stimulus enhancement) and 46.2% external noise exclusion across the training sessions. This 12-parameter model is statistically equivalent to the most saturated model that assumes all three mechanisms of perceptual learning ($p > 0.20$) and is superior to all its subset models ($p < 0.0001$). The parameters of the best fitting model and the relevant statistics are detailed in Table 2. The pattern of results replicated Lu and Doshier (1999) in an essentially identical task.

In the untrained eye, performance for the average observer deteriorated somewhat during transfer sessions. The TvC functions are best explained by a PTM that allowed A_{add} and A_{ext} to vary across sessions: this model

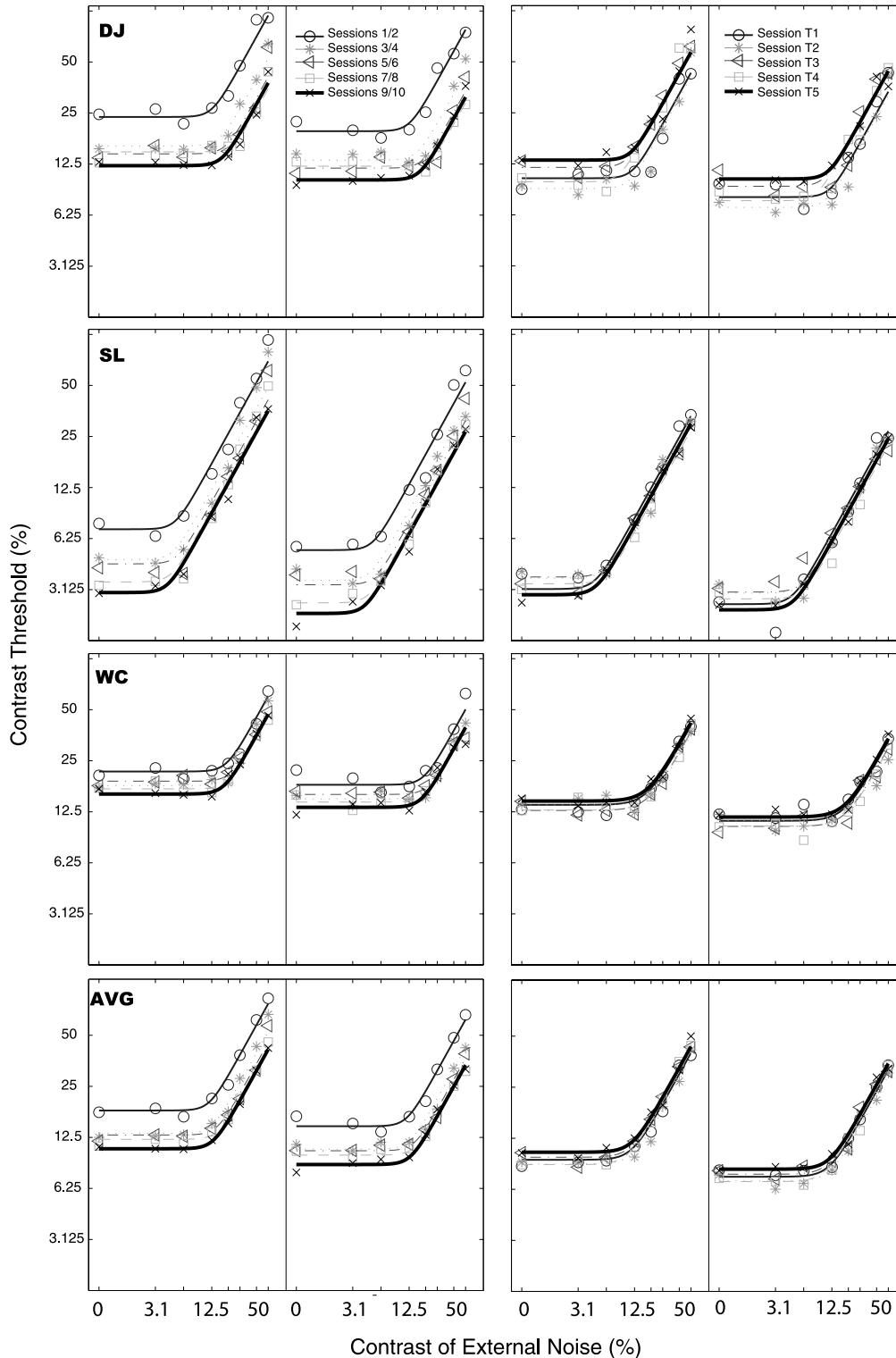


Fig. 4. TvC functions at two performance criterion levels (79.3% and 70.7% correct) in training (left panels) and transfer (right panels) sessions.

accounted for 99.2% of the variance in the average data with $A_{add} = 1.0, 0.8740, 1.084, 0.8571,$ and $1.273,$ and $A_{ext} = 1.0, 0.9247, 1.063, 1.036,$ and $1.090.$ No consistent downward trend was found in A_{add} or $A_{ext}.$

In summary, performance in the trained eye was improved via a mixture of stimulus enhancement and template retuning. Virtually no further learning was found in the untrained eye during five transfer sessions. The

Table 2
Parameters of the best fitting PTM's

Parameter	Training				Transfer			
	DJ	SL	WC	AVG	DJ	SL	WC	AVG
N_{mul}	0.4015	0.5198	0.3458	0.4408	0.4964	0.3785	0.1887	0.3660
N_{add}	5.80E-04	4.04E-05	2.06E-03	4.89E-04	5.12E-04	8.79E-05	1.24E-02	2.49E-03
β	0.4549	0.7047	0.6933	0.5771	1.096	1.316	1.059	1.127
γ	3.000	3.000	2.898	2.989	3.000	2.703	1.999	2.346
$A_{mul}(2)$	1	1	1	1	1	1	1	1
$A_{add}(2)$	0.3074	0.2905	0.5729	0.3945	0.6584	1.498	1.003	0.874
$A_{ext}(2)$	0.5586	0.7038	0.8265	0.6844	0.9490	0.8948	0.8768	0.9247
$A_{mul}(3)$	1	1	1	1	1	1	1	1
$A_{add}(3)$	0.2224	0.2438	0.6839	0.3700	1.5571	1.559	0.8594	1.0841
$A_{ext}(3)$	0.4342	0.5931	0.7859	0.5907	1.3483	0.922	0.9179	1.0628
$A_{mul}(4)$	1	1	1	1	1	1	1	1
$A_{add}(4)$	0.2406	0.1167	0.5054	0.3102	0.866	1.215	0.8677	0.8571
$A_{ext}(4)$	0.3695	0.5412	0.7784	0.5443	1.316	0.8271	0.9074	1.036
$A_{mul}(5)$	1	1	1	1	1	1	1	1
$A_{add}(5)$	0.1376	0.0758	0.4121	0.2116	2.095	0.8116	1.108	1.273
$A_{ext}(5)$	0.4004	0.5108	0.7823	0.5384	1.322	0.902	1.039	1.090
r^2	0.9751	0.9818	0.9829	0.9914	0.9684	0.9896	0.9826	0.9921
df	68	68	68	68	68	68	68	68
$F(4, 64)$	0.2241 ^{ns}	0.9391 ^{ns}	0.7254 ^{ns}	0.3866 ^{ns}	0.3223 ^{ns}	1.868 ^{ns}	2.069 ^M	2.039 ^M
$F(4, 68)$	93.05 [#]	28.78 [#]	8.647 [#]	80.07 [#]	11.93 [#]	4.148 [*]	2.778 [^]	4.784 [^]
$F(4, 68)$	25.79 [#]	13.47 [#]	13.83 [#]	38.58 [#]	5.327 [†]	2.623 [^]	2.056 ^M	3.874 [*]
$F(8, 68)$	54.57 [#]	22.15 [#]	13.15 [#]	70.63 [#]	7.519 [#]	2.902 [*]	2.896 [*]	4.976 [#]

^M $p > 0.05$.

^{ns} $p > 0.10$.

^{*} $p < 0.01$.

[†] $p < 0.001$.

[^] $p < 0.05$.

[#] $p < 0.0001$.

results suggest that perceptual learning of Gabor orientation identification in one eye involved two mechanisms, both of which transferred completely to the other, untrained eye.

4. Summary and discussion

Perceptual learning in a variety of tasks has been evaluated for specificity (or conversely, transfer) to retinal position (Ahissar & Hochstein, 1996; Berardi & Fiorentini, 1987; Karni & Sagi, 1991; Schoups et al., 1995; Shiu & Pashler, 1992), eye of training (Ahissar & Hochstein, 1996; Ball & Sekuler, 1987; Fahle & Edelman, 1993; Fiorentini & Berardi, 1981; Karni & Sagi, 1991; Schoups & Orban, 1996), orientation or spatial frequency (Fiorentini & Berardi, 1981; Karni & Sagi, 1991; Liu & Vaina, 1998; Liu & Weinshall, 2000; Shiu & Pashler, 1992), and retinal size (Ahissar & Hochstein, 1996; Fiorentini & Berardi, 1981; Lu & Doshier, 2004). In many cases, the observed patterns of transfer and/or specificity in combination with known properties of visual system have led to implications about the neural mechanisms and locus of learning. For example, location specificity is associated by some (e.g., Karni & Sagi, 1991) with ear-

ly locus in the visual system, perhaps V1, with small receptive fields (but see (Mollon & Danilova, 1996) for a critique). Orientation specificity is also often associated with early visual areas (V1, V2). On the other hand, performance improvements may reflect a number of different mechanisms that could potentially operate at different levels of the visual system (Doshier & Lu, 1998, 1999; Lu & Doshier, 2004). Investigating joint patterns of transfer and learning mechanisms may allow us to relate transfer to each specific mechanism and provide significant structural constraints on inferred locus of learning.

In this study, we combined transfer tests with external noise manipulations and the Perceptual Template Model to investigate the eye-specificity of mechanisms of perceptual learning in peripheral Gabor orientation identification. We found that monocular learning improved performance (reduced contrast thresholds) with virtually equal magnitude across a wide range of external noise levels with no significant change in central task performance. The learning effects were fully accounted for by a mechanism consisted of a mixture of stimulus enhancement and template re-tuning. The results completely replicated those of Doshier and Lu (1998, 1999) in an identical Gabor orientation identification task.

The effects of perceptual learning in the trained eye generalized completely to the untrained eye, indicated both by the comparable levels of performance in the last session of the trained eye and the first session of the transfer test in the untrained eye, and by the absence of subsequent learning in the untrained eye during transfer sessions.

The transfer results in high external noise conditions are completely consistent with previous studies on eye-specificity of learning in orientation discrimination in noisy displays (Schoups et al., 1995). The complete transfer of learning in zero and low external noise conditions, however, is very different from what we found in perceptual learning of identifying the direction of moving luminance-defined objects, where a substantial amount of eye-specificity was found in clear and low external noise displays (Lu et al., 2005). Combining our results with the known physiology of binocular coding of orientation (Livingstone & Hubel, 1984; Blasdel, 1992), we suggest that the site for perceptual learning of Gabor orientation identification resides in areas post layer 4Cb of the primary visual cortex. This conclusion is largely consistent with observations of learning only post layer 4 in V1 by Schoups, Vogels, Qian, and Orban (2001) and relatively small magnitude of learning in V1 neurons (Ghose, Yang, & Maunsell, 2002) but relatively large amount of learning in largely binocular V4 neurons (Ghose et al., 2002; Yang & Maunsell, 2004) when the monkeys performed orientation discrimination tasks.

Acknowledgment

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 & Doshier, 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 are 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 & Doshier, 1999): 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 imple-

mented by multiplying the corresponding noise² in the PTM with learning parameters $A_{\text{add}}(t)$, $A_{\text{ext}}(t)$, and $A_{\text{mul}}(t)$ in each training block t , with $A_{\text{add}}(1) = A_{\text{ext}}(1) = A_{\text{mul}}(1) = 1.0$ (Doshier & Lu, 1998, 1999; Lu & Doshier, 2004). In the most saturated PTM with all three mechanisms of perceptual learning, thresholds are expressed as functions of external noise by the following equation:

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

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

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

where \sum and $\text{mean}()$ 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

$$F(\text{df}_1, \text{df}_2) = \frac{(r_{\text{full}}^2 - r_{\text{reduced}}^2)/\text{df}_1}{(1 - r_{\text{full}}^2)/\text{df}_2}, \quad (\text{A.3})$$

where $\text{df}_1 = k_{\text{full}} - k_{\text{reduced}}$, and $\text{df}_2 = N - k_{\text{full}}$. The k 's are the number of parameters in each model, and N is the number of predicted data points.

References

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

² In the PTM, stimulus enhancement is mathematically equivalent to internal additive noise reduction (Lu & Doshier, 1998).

- Anderson, J. R., & Fincham, J. M. (1994). Acquisition of procedural skills from examples. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, 20(6), 1322–1340.
- Ball, K., & Sekuler, R. (1982). A specific and enduring improvement in visual motion discrimination. *Science*, 218(4573), 697–698.
- Ball, K., & Sekuler, R. (1987). Direction-specific improvement in motion discrimination. *Vision Research*, 27(6), 953–965.
- Beard, B. L., Levi, D. M., & Reich, L. N. (1995). Perceptual learning in parafoveal vision. *Vision Research*, 35(12), 1679–1690.
- Berardi, N., & Fiorentini, A. (1987). Interhemispheric transfer of visual information in humans: Spatial characteristics. *Journal of Physiology*, 384, 633–647.
- Blasdel, G. G. (1992). Orientation selectivity, preference, and continuity in monkey striate cortex. *Journal of Neuroscience*, 12(8), 3139–3161.
- Blasdel, G. G., & Fitzpatrick, D. (1984). Physiological organization of layer 4 in macaque striate cortex. *Journal of Neuroscience*, 4(3), 880–895.
- Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, 10(4), 433–436.
- Chung, S. T. L., Levi, D. M., & Tjan, B. S. (2001). Perceptual learning. *Optical Express*, 9.
- De Luca, E., & Fahle, M. (1999). Learning of interpolation in 2 and 3 dimensions. *Vision Research*, 39(12), 2051–2062.
- Dorais, A., & Sagi, D. (1997). Contrast masking effects change with practice. *Vision Research*, 37(13), 1725–1733.
- Dosher, B. A., & Lu, Z.-L. (1998). Perceptual learning reflects external noise filtering and internal noise reduction through channel reweighting. *Proceedings of the National Academy of Sciences of the United States of America*, 95(23), 13988–13993.
- Dosher, B. A., & Lu, Z.-L. (1999). Mechanisms of perceptual learning. *Vision Research*, 39(19), 3197–3221.
- Fahle, M. (1994). Human pattern recognition: Parallel processing and perceptual learning. *Perception*, 23(4), 411–427.
- 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.
- Fahle, M., Edelman, S., & Poggio, T. (1995). Fast perceptual learning in hyperacuity. *Vision Research*, 35(21), 3003–3013.
- Fiorentini, A., & Berardi, N. (1981). Learning in grating waveform discrimination: Specificity for orientation and spatial frequency. *Vision Research*, 21(7), 1149–1158.
- Ghose, G. M., Yang, T., & Maunsell, J. H. R. (2002). Physiological correlates of perceptual learning in monkey V1 and V2. *Journal of Neurophysiology*, 87(10), 1867–1888.
- Gold, J., Bennett, P. J., & Sekuler, A. B. (1999). Signal but not noise changes with perceptual learning. *Nature*, 402(6758), 176–178.
- Griffiths, F., & Chubb, C. (1995). Perceptual learning of motion. *Investigative Ophthalmology & Visual Science*, 36(4), S377.
- Hawken, M. J., & Parker, A. J. (1984). Contrast sensitivity and orientation selectivity in lamina IV of the striate cortex of Old World monkeys. *Experimental Brain Research*, 54(2), 367–372.
- Hubel, D. H., Wiesel, T. N., & Stryker, M. P. (1977). Orientation columns in macaque monkey visual cortex demonstrated by the 2-deoxyglucose autoradiographic technique. *Nature*, 269(5626), 328–330.
- Juttner, M. (2001). Dissociation of pattern discrimination and categorization in extrafoveal vision. *The 17th Annual Meeting of the International Society for Psychophysics* (Vol. 17, pp. 444–449). Leipzig, Germany: The International Society For Psychophysics.
- Karni, A., & Bertini, G. (1997). Learning perceptual skills: Behavioral probes into adult cortical plasticity. *Current Opinion in Neurobiology*, 7(4), 530–535.
- 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.
- Levitt, H. (1971). Transformed up-down methods in psychoacoustics. *Journal of the Acoustical Society of America*, 49(2, Pt. 2), 467–477.
- Li, R. W., Levi, D. M., & Klein, S. A. (2003). Perceptual learning improves efficiency by re-tuning the “template” for position discrimination. *Nature Neuroscience*, 7, 178–183.
- Li, X., Lu, Z.-L., Xu, P., Jin, J., & Zhou, Y. (2003). Generating high gray-level resolution monochrome displays with conventional computer graphics cards and color monitors. *Journal of Neuroscience Methods*, 130, 9–18.
- Liu, Z., & Vaina, L. M. (1998). Simultaneous learning of motion discrimination in two directions. *Cognitive Brain Research*, 6(4), 347–349.
- Liu, Z., & Weinshall, D. (2000). Mechanisms of generalization in perceptual learning. *Vision Research*, 40(1), 97–109.
- Livingstone, M. S., & Hubel, D. H. (1984). Specificity of intrinsic connections in primate Primary visual cortex. *Journal of Neuroscience*, 4(11), 2830–2835.
- Logan, G. D. (1988). Toward an instance theory of automatization. *Psychological Review*, 95(4), 492–527.
- Lu, Z.-L., Chu, W., Dosher, B., & Lee, S. (2005). Independent perceptual learning in monocular and binocular motion systems. *Proceedings of the National Academy of Sciences of the United States of America*, 102, 5624–5629.
- Lu, Z.-L., & Dosher, B. A. (1998). External noise distinguishes attention mechanisms. *Vision Research*, 38(9), 1183–1198.
- Lu, Z.-L., & Dosher, B. A. (1999). Characterizing human perceptual inefficiencies with equivalent internal noise. *Journal of the Optical Society of America A—Optics Image Science and Vision*, 16(3), 764–778.
- Lu, Z.-L., & Dosher, B. A. (2004). Perceptual learning retunes the perceptual template in foveal orientation identification. *Journal of Vision*, 4, 44–56.
- Mathworks, I. (1998). Matlab, 5.2.
- Mollon, J. D., & Danilova, M. V. (1996). Three remarks on perceptual learning. *Spatial Vision*, 10(1), 51–58.
- 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(7–8), 1337–1350.
- Poggio, T., Fahle, M., & Edelman, S. (1992). Fast perceptual learning in visual hyperacuity. *Science*, 256(5059), 1018–1021.
- Reeves, A., & Sperling, G. (1986). Attention gating in short-term visual memory. *Psychological Review*, 93(2), 180–206.
- Saarinen, J., & Levi, D. M. (1995). Perceptual learning in vernier acuity: What is learned? *Vision Research*, 35(4), 519–527.
- Sagi, D., & Tanne, D. (1994). Perceptual-learning—learning to see. *Current Opinion in Neurobiology*, 4(2), 195–199.
- Schoups, A., Vogels, R., Qian, N., & Orban, G. (2001). Practising orientation identification improves orientation coding in V1 neurons. *Nature*, 412(6846), 549–553.
- Schoups, A. A., & Orban, G. A. (1996). Interocular transfer in perceptual learning of a pop-out discrimination task. *Proceedings of the National Academy of Sciences of the United States of America*, 93(14), 7358–7362.
- Schoups, A. A., Vogels, R., & Orban, G. A. (1995). Human perceptual learning in identifying the oblique orientation: Retinotopy, orientation specificity and monocularity. *Journal of Physiology*, 483, 797–810.
- 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.

- Sireteanu, R., & Rettenbach, R. (1995). Perceptual learning in visual search: Fast, enduring, but non-specific. *Vision Research*, 35(14), 2037–2043.
- Sireteanu, R., & Rettenbach, R. (2000). Perceptual learning in visual search generalizes over tasks, locations, and eyes. *Vision Research*, 40(21), 2925–2949.
- Sowden, P. T., Rose, D., & Davies, I. R. L. (2002). Perceptual learning of luminance contrast detection: Specific for spatial frequency and retinal location but not orientation. *Vision Research*, 42(10), 1249–1258.
- SPSS, I. (1999). SPSS for Windows, Chicago, Illinois.
- Tjan, B. S., Chung, S., & Levi, D., (2002). Limitation of ideal-observer analysis in understanding perceptual learning. In *Twenty-seventh annual interdisciplinary conference, Jackson Hole, Wyoming*. Available from http://aris.ss.uci.edu/HIPLab/AIC/abs.aic02_abc.htm.
- Tootell, R. B., Hamilton, S. L., Silverman, M. S., & Switkes, E. (1988). Functional anatomy of macaque striate cortex. I. Ocular dominance, binocular interactions, and baseline conditions. *Journal of Neuroscience*, 8(5), 1500–1530.
- Vaina, L. M., Sundareswaran, V., & Harris, J. G. (1995). Learning to ignore: Psychophysics and computational modeling of fast learning of direction in noisy motion stimuli. *Cognitive Brain Research*, 2(3), 155–163.
- Yang, T., & Maunsell, J. H. R. (2004). The effect of perceptual learning on neuronal responses in monkey visual area V4. *Journal of Neuroscience*, 24(7), 1617–1626.