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Perceptual learning in monocular pattern masking: Experiments and explanations by the twin summation gain control model of contrast processing

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We investigated practice effects on contrast thresholds for target patterns. Results showed that practice decreased contrast thresholds when targets were presented on maskers. Thresholds tended to decrease more at the higher end of the masker contrast range. At least partially, learning transferred to stimuli of the untrained phase. We simulated changes in threshold versus contrast functions using a contrast-processing model and then fit the model to pre- and posttraining data. The simulation results and model fit suggest that learning in pattern masking can be accounted for by changes in nonlinear transducer functions for divisive inhibitory signals.

Perceptual learning refers to "any relatively permanent and consistent change in the perception of a stimulus array following practice or experience with this array" (Gibson, 1963, p. 29). Since the 1970s, many studies have examined perceptual learning based on simple stimuli and tasks (for reviews, see Ahissar & Hochstein, 1998; Fahle & Poggio, 2002). These studies investigated stimulus change in relation to various dimensions, including orientation, retinal position, spatial frequency, and the eye to which stimuli were presented. For example, Ball and Sekuler (1987) reported that the ability to discriminate similar directions of motion gradually improved with practice, but also noted that this improvement did not transfer to the direction opposite that of the training condition. Shiu and Pashler (1992) reported that the ability to discriminate the orientation of a pair of straight lines improved with practice; however, this improvement did not transfer to any untrained retinal position. Results from several similar studies also showed that improvements were specific to simple features of stimuli, suggesting that an aspect of perceptual learning reflects changes only in the low-level perceptual processing by which fundamental properties of visual stimuli are processed. Luminance contrast is considered one such fundamental property.

Luminance contrast affects performance in various visual tasks, such as the discrimination of motion speed (Stone & Thompson, 1992). It is relevant, therefore, to consider how contrast processing changes with practice. Several studies have shown that contrast thresholds for target patterns decreased with practice when target gratings were presented on masker gratings (Swift & Smith, 1983), when Gabor targets were presented on identical patterns (Yu, Klein, & Levi, 2004),[1] when Gabor targets were presented on identical patterns with flanking Gabor maskers (Adini, Sagi, & Tsodyks, 2002), and when Gabor targets were presented on a combination of two Gabor maskers, the orientations of which were different from the target's orientation (Dorais & Sagi, 1997; Zenger & Sagi, 1996). As for learning on contrast detection thresholds (with no masker), two studies reported that contrast detection thresholds decreased with practice (Sowden, Rose, & Davies, 2002; Yu et al., 2004), whereas two other studies found no learning effect (Dorais & Sagi, 1997; Zenger & Sagi, 1996).

Previous studies have used different training durations. Swift and Smith (1983) trained observers for about 15 trials, whereas others trained observers over several days (Adini et al., 2002; Dorais & Sagi, 1997; Yu et al., 2004). There appear to be at least two types of learning: within-day and interday learning. Within-day learning occurs during a session lasting several minutes or hours, whereas interday learning gradually improves performance over the course of several days. The present study focused on interday learning only.

Contrast thresholds can be plotted as functions of the contrast of maskers and pedestals. Such functions are called *threshold versus contrast* (TvC) functions. TvC function has been found to have a dipper shape; that is,

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thresholds are lower at the lower ends of masker contrast ranges, but elevated at the higher ends of masker contrast ranges (Legge & Foley, 1980; Nachmias & Sansbury, 1974; Stromeyer & Klein, 1974). Results of previous studies also differ over whether slopes of TvC functions at the higher end of masker contrast ranges become less steep with practice (Adini et al., 2002; Dorais & Sagi, 1997) or not (Yu et al., 2004; Zenger & Sagi, 1996).

Dorais and Sagi (1997) examined the transfer of practice effects on contrast thresholds. Learning transferred to the untrained eye but did not transfer to targets with the untrained orientation. More complicated results were found for stimuli in the untrained phase. Learning did not transfer when the phase of one of the maskers was changed, but it did transfer when the phases of two maskers were transposed. Yu et al. (2004) also examined learning transfer and reported an interocular transfer of learning, similar to the results found by Dorais and Sagi (1997). In addition, Yu et al. (2004) found that learning partly transferred to the untrained retinal position and to the stimuli with an untrained spatial frequency, orientation, or contrast as well.

In short, previous studies have suggested that contrast thresholds for target patterns decrease with practice in the presence of maskers or pedestals, and that that learning transfers to some untrained stimulus conditions. The present study focused on those mechanisms that might exhibit learning in pattern masking. We conducted three experiments to investigate (1) whether practice decreases contrast thresholds when no maskers are presented, (2) how TvC functions change with practice, and (3) whether the practice effects transfer to the untrained eye and to stimuli with the untrained orientation or untrained phase. To consider the mechanisms of practice effects on contrast thresholds under pattern-masking conditions, we simulated changes in TvC functions using our own contrast-processing model (Maehara & Goryo, 2005)—called the *twin summation gain control model* by Meese, Georgeson, and Baker (2006)—and fit the model using pre- and post-training data obtained in this study. On the basis of the results of these simulations and model fitting, we propose a mechanism of learning in pattern masking.

GENERAL METHOD

Observers

There were 3 observers: N.S., K.S., and H.N. All had normal or corrected-to-normal visual acuity and no visual problems. None of the observers had experience in experiments in which contrast thresholds were measured.

Apparatus

Stimuli were generated using a Macintosh G3 computer and were displayed on a video monitor (Mitsubishi, RD21GH). A contrast resolution of up to 12-bit accuracy was obtained by combining the red, green, and blue outputs of a video card to drive the green gun of the monitor (the red and blue guns were blank; Pelli & Zhang, 1991). The display resolution was set to 1,024 × 768 pixels, with a refresh rate of 120 Hz. VideoToolbox, a set of C routines for visual psychophysics, was used for image generation and gamma correction (Pelli, 1997). Responses were entered on a keyboard and recorded by the computer.

Observers viewed the display through a mirror stereoscope and a rectangular tube. A vertical black septum halved the view of the monitor. Each half-field was 10º × 10º of the visual angle. Frames for the half-fields aided in precise binocular alignment. A chinrest held the viewing distance constant at 86 cm. The room was dark, except for ambient illumination provided by the monitor.

Stimuli

The stimulus field had a mean luminance of 30 cd/m^2. The Commission Internationale de l'Eclairage (CIE: International Commission on Illumination) chromaticity coordinates for the stimulus field were (0.291, 0.590). The target patterns were Gaussian-windowed sinusoidal gratings (Gabor patterns). The standard deviation of the Gaussian window function was 0.5º of the visual angle. The underlying sinusoidal gratings had a spatial frequency of 2 cpd. The orientation and phase of the gratings were independent variables. The underlying sinusoidal gratings were oriented at 45º or 135º in a 0º or 180º cosine phase at the center of the stimulus field. Target contrast was defined as the Michelson contrast of the gratings prior to attenuation by the Gaussian window. The masker patterns were sinusoidal gratings. Maskers had the same spatial frequency, orientation, and phase as did targets. The visual angle subtended by maskers was 7.75º × 7.75º. Targets and maskers were presented to one eye for four frames (33 msec); the other eye continued to view a uniform field of the same mean luminance. All contrasts are expressed in dB re 1, where 1 dB is 1/20 of a log unit of contrast.

Crosshairs consisting of four thin lines were always binocularly present, to indicate the center of the stimulus field and to aid in precise binocular alignment. The two vertical lines were present at the upper and lower portions of the stimulus field, and the two horizontal crosshairs were present at the left and right portions. The innermost edges of these lines were 3.875º from the center of the stimulus field, so that the crosshairs did not mask the targets. The crosshairs had a luminance of 77.8 cd/m^2.

Procedure

Target contrast thresholds were measured using a two-interval, forced choice procedure. Observers completed one session a day. At the beginning of each session, observers acclimated to the mean luminance of the stimulus field for 5 min. Observers fixated on the center of the stimulus field throughout each trial sequence, during which the target was presented in either the first or the second of two 33-msec observation intervals, with a blank interval of 1,100 msec between them. The target interval was determined randomly, with the probability of presentation of any given target for each interval being .5. Maskers were presented for both intervals, except in Experiment 1, in which no maskers were presented. A tone indicated the beginning of each interval. Observers were required to report whether targets were presented in the first or second interval. When the observer made a mistake, feedback was given in the form of a beep.

A one-up/three-down staircase was used to adjust the target contrast. The step size of each staircase was initially set at 4 dB, then moved to 2 dB after the second reversal. Contrast thresholds were measured using interleaved pairs of staircases. Each staircase terminated after 12 reversals. Target contrast thresholds were calculated by taking the average of target contrasts at the last 10 reversals for each staircase—that is, 20 reversals for each threshold. This method has established thresholds at 79% correct detection (Levitt, 1971).

EXPERIMENT 1

Inconsistent results have been reported about whether contrast thresholds decrease with practice when no maskers were presented (Adini et al., 2002; Dorais & Sagi, 1997; Yu et al., 2004). Therefore, we began with an examination of the effects of practice on contrast thresholds for targets in the absence of maskers.

Method

In a single experimental session, interleaved pairs of staircases were used to track the target contrast thresholds for four types of targets. Maskers were not presented in Experiment 1. One target type was identical to those used later—in Experiment 2—when we examined practice effects on thresholds for targets in the presence of maskers. We use the term *training condition* to refer to the stimulus condition in which targets of this type were presented. The other three target types differed from the training-condition targets by either 180º in phase, 90º in orientation, or the eye to which targets were presented (i.e., phase-changed, orientation-changed, or eye-changed condition, respectively). With respect to the stimulus conditions, measurements were taken in blocks. Observers were shown four blocks in pseudorandom order. Resting times of more than 30 sec were provided between blocks. Observers participated in one session a day. Each session required approximately 45 min for completion.

Targets in the training condition were different for each observer. Under the training condition for Observer N.S., targets were presented to the right eye at a 135º orientation and 0º phase at the center of the stimulus field. For Observer K.S., targets were presented to the left eye at a 45º orientation and 180º phase at the center of the stimulus field. For Observer H.N., targets were presented to the right eye at a 45º orientation and 0º phase at the center of the stimulus field.

Results and Discussion

Figure 1 shows the contrast thresholds for targets across several days of training. Observers N.S. and K.S. showed little difference in their mean thresholds for the four conditions between Session 1 (N.S., −25.9 dB; K.S., −28.2 dB) and Session 4 (N.S., −25.8 dB; K.S., −29.0 dB). For H.N., the mean thresholds were lower in Session 4 (−27.3 dB) than in Session 1 (−25.0 dB) by 2.3 dB. To investigate whether this decrease in thresholds could be attributed to learning, H.N. participated in additional sessions. However, as is indicated in Figure 1, H.N.'s measurements were relatively unstable, and there was little difference in the mean thresholds between Session 1 (−25.0 dB) and Session 9 (−25.1 dB). Therefore, the decrease in thresholds for H.N. between Sessions 1 and 4 could not be attributed to learning. These results from the 3 observers suggest that contrast thresholds do not decrease with practice when maskers are not presented. These results agree with those reported by Dorais and Sagi (1997) and Adini et al. (2002).

There were few differences among the four stimulus conditions, except for the eye-changed condition for N.S. As is shown in Figure 1, thresholds for N.S. were always higher in the eye-changed condition (−24.4 dB on average) than in the training condition (−26.7 dB on average). This result may be due to a difference in contrast sensitivity between the left eye and the right eye—that is, N.S. may have been more sensitive to stimuli presented to the right eye than to those presented to the left eye.

Thresholds in the present experiment were comparably higher than those reported in previous studies (Adini et al., 2002; Dorais & Sagi, 1997; Yu et al., 2004). We presented stimuli to one eye at a time, whereas most previous studies presented stimuli to both eyes simultaneously. It seems that this difference may have caused the higher thresholds. The difference in thresholds may also be attributable to differences in the spatial frequency of targets. Moreover, durations of targets were shorter in the present experiment (33 msec) than in previous studies (around 100 msec).

EXPERIMENT 2

In this experiment, we examined how TvC functions changed with practice. The targets were the same Gabor patterns as those used in Experiment 1. However, unlike in Experiment 1, sinusoidal gratings were presented as maskers. Targets and maskers were simultaneously presented to one eye. Maskers had the same orientation and phase as targets. Observers participated in Experiment 2 after having participated in Experiment 1.

Method

In a single experimental session, interleaved pairs of staircases were used to track the target contrast thresholds for 11 masker contrasts (−∞, −46, −42, −38, −34, −30, −26, −22, −18, −14, and −10 dB). The measurements were blocked with respect to masker contrast. Observers were first given a block of −∞ dB (no masker), and then were given the remaining blocks in pseudorandom order. Approximately 1,400 trials were run per session. Each session required approximately 105 min for completion. Observers participated in one session a day. The experiment ended if thresholds for the 11 masker contrasts were not lower than the previously lowest

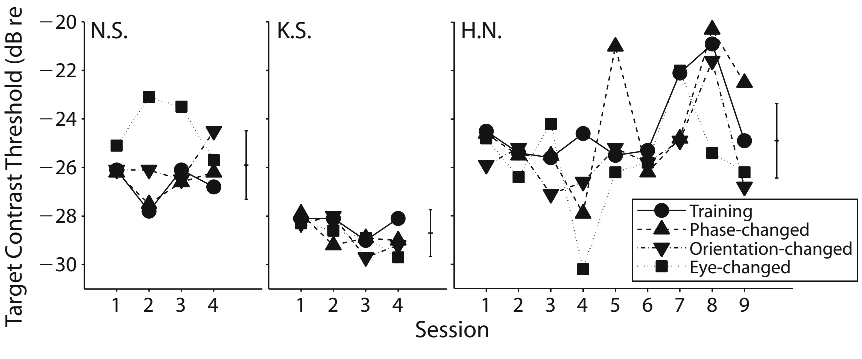

Figure 1. Contrast thresholds for targets in the absence of maskers during several days of training in Experiment 1. The thresholds did not decrease with practice. As compared with the training condition, the other three conditions differed in terms of target phase, target orientation, or the eye to which targets were presented. Error bars depict grand mean thresholds and mean 95% confidence intervals over four conditions.

thresholds by more than 1 dB. The conditions of the stimuli (orientation, phase, and presentation eye) were fixed during Experiment 2.

Results and Discussion

N.S., K.S., and H.N. participated in eight, six, and seven sessions, respectively. Figure 2 plots target contrast thresholds for masker contrasts of −22 dB to −10 dB. Thresholds gradually decreased with practice. Thresholds for masker contrasts of less than −22 dB are not included in Figure 2 for reasons of clarity; these thresholds had similar values and showed little decrease in thresholds.

Target contrast thresholds in the first session were considered to be pretraining thresholds. The medians of thresholds in the last three sessions were considered to be posttraining thresholds. Figure 3 shows TvC functions for the pre- and posttraining data. Pre- and posttraining thresholds were subjected to a 2 × 10 (training × masker contrast) repeated measures ANOVA. Thresholds for $-\infty$ dB were excluded from this ANOVA because Experiment 1 had suggested that practice produced no learning when no maskers were presented. Thresholds were lower for posttraining than for pretraining, producing a significant main effect of training [$F(1,2) = 19.4$, $MS_e = 1.52$, $p = .048$]. This result suggests that the contrast thresholds for targets decreased with practice in the presence of maskers. The masker contrast main effect was also significant [$F(9,18) = 38.8$, $MS_e = 4.17$, $p < .001$].

For Observers N.S. and K.S., slopes of the TvC functions for the masker contrasts of −26 dB to −10 dB were steeper for pretraining (0.92 and 0.90, respectively) than for posttraining (0.67 and 0.67, respectively). This means that the higher the contrast of maskers, the greater the decrease in thresholds, although the training × masker contrast interaction was not significant ($p = .212$).[2] Results for N.S. and K.S. agree with previous findings, in which slopes became less steep with practice (Adini et al., 2002; Dorais & Sagi, 1997). However, the results for H.N. showed little difference in pre- (0.71) and posttraining (0.72) slopes. The results for H.N. agree with those reported by Yu et al. (2004).

Results for H.N. differed from those of the other observers in some other aspects as well. As was noted above, slopes of TvC functions did not change with practice. The thresholds for H.N. were generally higher than thresholds for other observers. In addition, thresholds for H.N. were higher at masker contrasts of −46 dB to −38 dB than at a masker contrast of $-\infty$. The causes of these differences are unclear. In comparison with the other observers, H.N. had little experience with psychological experiments. It is possible that H.N. learned the task in a different way than did the other observers.

EXPERIMENT 3

In Experiment 3, we examined whether practice effects on contrast thresholds transferred to untrained stimuli that differed from the trained stimuli in phase, orientation, or presentation eye. Observers participated in Experiment 3 after having participated in Experiment 2.

Method

There were four types of conditions—trained, phase-changed, orientation-changed, and eye-changed conditions, as in Experiment 1. In the trained condition, stimuli were the same as those used in Experiment 2. In the phase-changed condition, the phases of the stimuli differed from those of the trained stimuli by 180º. In the orientation-changed condition, the stimuli orientation differed from that of the trained stimuli by 90º. In the eye-changed condition, stimuli were presented to the untrained eye. Maskers had the same orientation and phase as targets. Targets and maskers were presented to one eye.

Session sequences were identical to those in Experiment 2. In a single experimental session, interleaved pairs of staircases were used to track the target contrast thresholds for 11 masker contrasts ($-\infty$, −46, −42, −38, −34, −30, −26, −22, −18, −14, and −10 dB). The measurements were blocked with respect to masker contrast. Observers were first given a block of $-\infty$ dB (no masker), and then were given the remaining blocks in pseudorandom order.

A given session was devoted to one of the four stimulus conditions. Observers participated in sessions for the phase-changed condition, the orientation-changed condition, the eye-changed condition, and the trained condition, in that order. Trained-condition sessions were conducted in order to examine whether learning was preserved after the tests, thus allowing learning transfer. Observers participated in one session a day. Each session required approximately 105 min to complete.

Results and Discussion

The following analysis focused on thresholds at masker contrasts of −26 dB to −10 dB and excluded thresholds

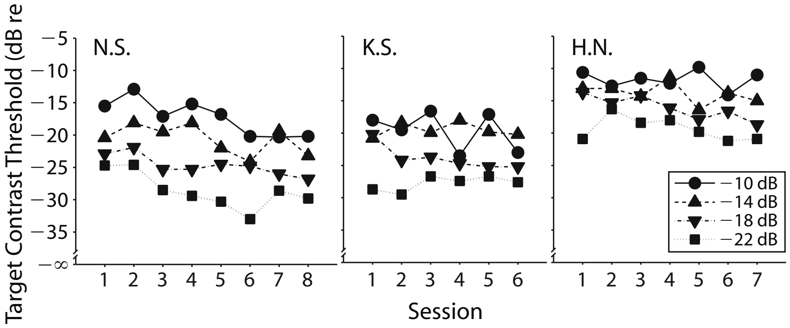

Figure 2. The time course of threshold decrease for masker contrasts of −22 dB to −10 dB. Thresholds gradually deceased with practice.

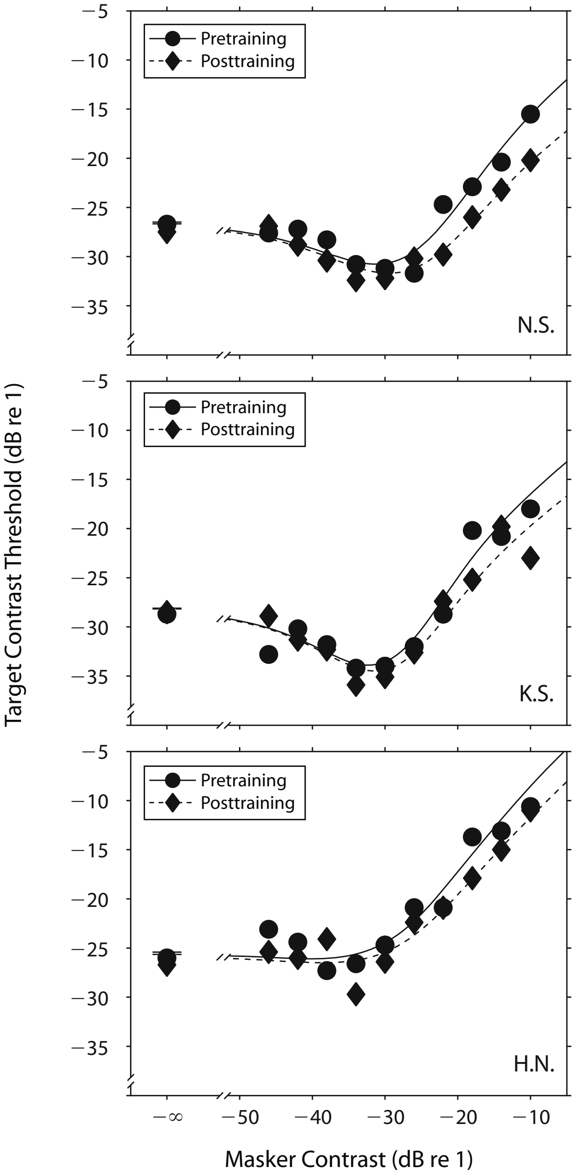

Figure 3. Threshold versus contrast functions for the pre- and posttraining data. Thresholds for the pre- and posttraining data differed at the higher end of the masker contrast range. The smooth curves correspond to the best fit of the model.

at masker contrasts of under −26 dB, because the practice effects on thresholds tended to be larger at the higher end of the masker contrast range. We express the degree of learning transfer for each condition as a fraction of the posttraining improvement obtained in Experiment 2. That is, for each masker contrast, threshold differences between pretraining and each condition were divided by a threshold difference between pre- and posttraining. Values of this fraction were then averaged over the masker contrast for each observer. We call these values *transfer rates*. If the threshold difference between pre- and posttraining was less than 0.5 dB, or if thresholds were higher for posttraining than for pretraining, we excluded the associated fraction value from the averaging. Figure 4 shows transfer rates for each condition.

For the phase-changed condition, the mean transfer rate was 0.64, with a 95% confidence interval of 0.27–1.01. Since the lower bound of the confidence interval was above 0, it is suggested that learning was at least partly transferred to the stimuli with the untrained phase. We also see, in Figure 5, that most of the thresholds for the phase-changed condition were lower than those for pretraining and higher than those for posttraining at the higher end of the masker contrast range. Dorais and Sagi (1997) also examined the transfer of learning to stimuli with the untrained phase. However, their experiments were different from ours, in that they used combinations of two Gabor patterns as maskers. Previous studies had not reported that learning transferred to stimuli with the untrained phase when targets and maskers had the same phase, orientation, and spatial frequency.

Results differed among observers for the orientation-changed condition. Learning transferred to the untrained orientation for N.S. (transfer rate = 1.01), whereas learning did not transfer for K.S. (transfer rate = −0.10). For H.N., the learning transfer rate was 1.05. However, the results were difficult to interpret, because thresholds for the orientation-changed condition were much higher than those for other conditions at the lower end of the masker contrast range (Figure 6, lower panel).

Figure 7 shows TvC functions for the eye-changed condition. For N.S., thresholds for the eye-changed condition were higher than those for other conditions at all masker contrasts (top panel). As was noted for Experiment 1, N.S. may have been more sensitive to stimuli presented to the right eye than to the left eye. This sensitivity difference would cause the difference in thresholds between the eye-changed condition and the other conditions. Therefore, for N.S., it is not clear whether learning transferred to the untrained eye. Learning did not transfer for K.S. (transfer rate = 0.02), whereas it almost transferred for H.N.

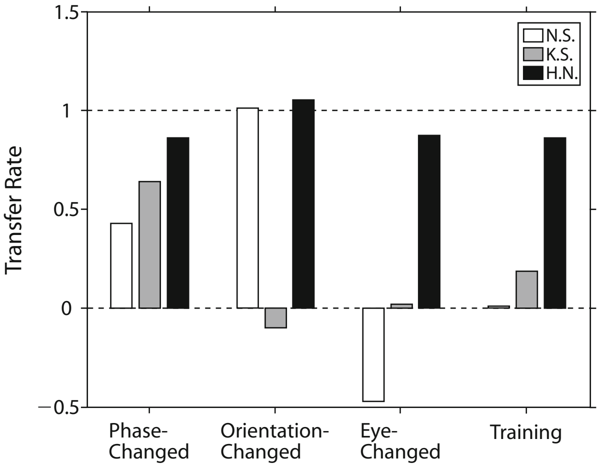

Figure 4. Mean transfer rates. If transfer rates were 1, learning was considered to have been transferred. If transfer rates were 0, learning was considered not to have been transferred.

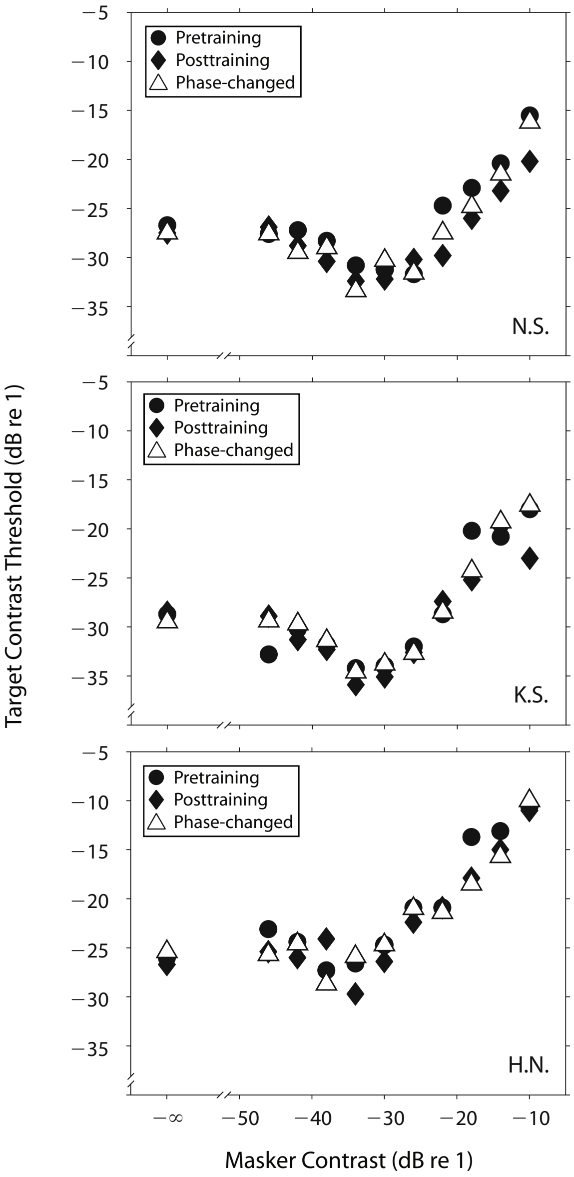

Figure 5. Threshold versus contrast functions for the phase-changed condition. Under this condition, the stimuli differed from the trained stimuli by a phase of 180º.

(transfer rate = 0.87). Therefore, results differed among observers for the eye-changed condition.

The results also showed interobserver differences in the posttest preservation of learning (Figure 8). Preservation of learning was evaluated in the same way that learning transfer was. Learning was barely preserved for N.S. and K.S. (preservation rate = 0.01 and 0.19, respectively), whereas learning was partly preserved for H.N. (preservation rate = 0.86). Although the reasons for these differences in learning preservation are unclear, the difference may reflect a disruption caused by subsequent learning. According to Seitz et al. (2005), performance of a subsequent task can disrupt prior perceptual learning. Researchers have also reported that practicing contrast discrimination produced no substantial learning when maskers with different contrasts were interleaved within a block (Adini, Wilkonsky, Haspel, Tsodyks, & Sagi, 2004; Yu et al., 2004). Thus, for N.S. and K.S., learning may have been disrupted by postpractice sessions, in which the observers performed the task for the untrained stimulus conditions.

SIMULATIONS AND MODEL FITTING

This section first presents an overview of the twin summation gain control model. Changes in TvC functions are then simulated using the model. Finally, the model is fit to

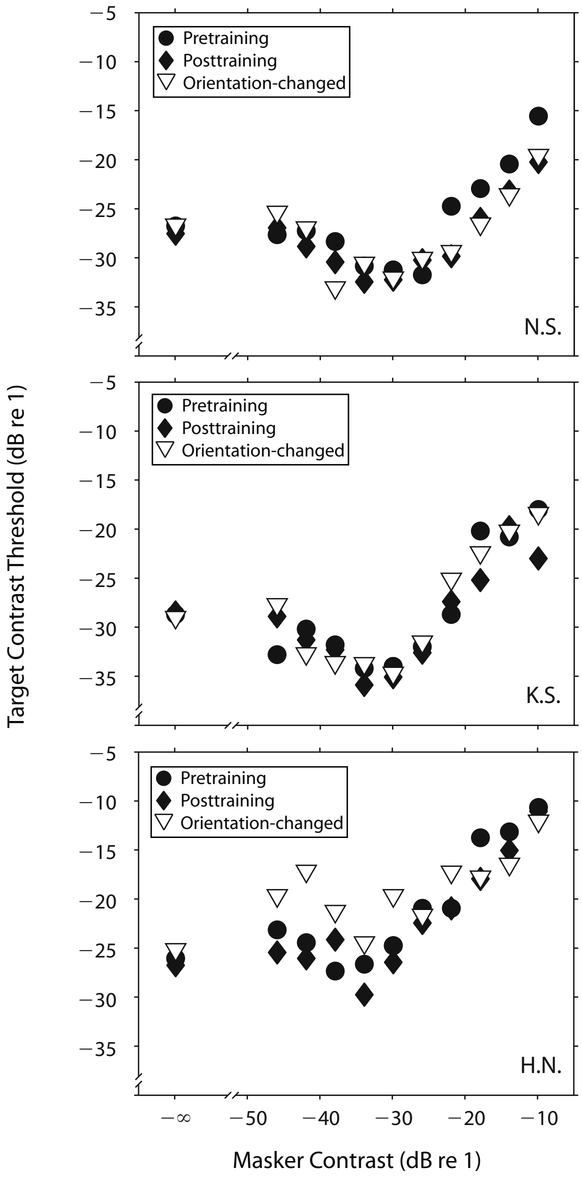

Figure 6. Threshold versus contrast functions for the orientation-changed condition. Under this condition, the stimuli differed from the trained stimuli by 90º.

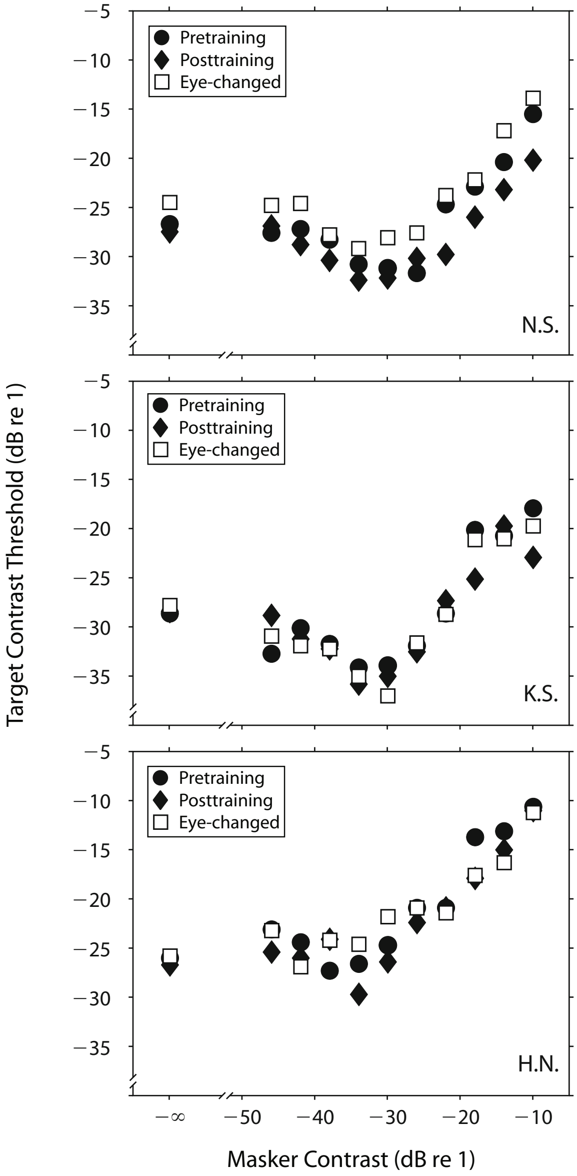

Figure 7. Threshold versus contrast functions for the eye-changed condition. Under this condition, stimuli were presented to the untrained eye.

the pre- and posttraining data, and mechanisms of learning in pattern masking are discussed.

Overview of the Twin Summation Gain Control Model of Contrast Processing

The twin summation gain control model is a revised version of Foley's model (Foley, 1994; Foley & Chen, 1999) and was originally designed to account for TvC functions in binocular, monocular, and dichoptic pattern masking (Maehara & Goryo, 2005).[3] Figure 9 schematically illustrates the model, which is briefly described below (for additional details, see Maehara & Goryo, 2005).

In the twin summation gain control model, linear operators are applied to the stimulus pattern presented to each eye. These linear operators have a linear spatial sensitivity function, expressed as a Gaussian windowed cosine, and are most sensitive to a pattern with a specific phase, orientation, and spatial frequency. It is assumed that there are many mechanisms tuned to different phases, orientations, and spatial frequencies. However, we show only one mechanism here, because, in the present study, targets and maskers had the same phase, orientation, and spatial frequency.

Outputs of the linear operators are monocular excitations (E''_{ij}) and monocular inhibitory signals (I''_{ij}). The monocular excitation produced by pattern component i, which is presented to eye j, is

$$E''_{ij} = C_{ij} S_{Ei}, \qquad (1)$$

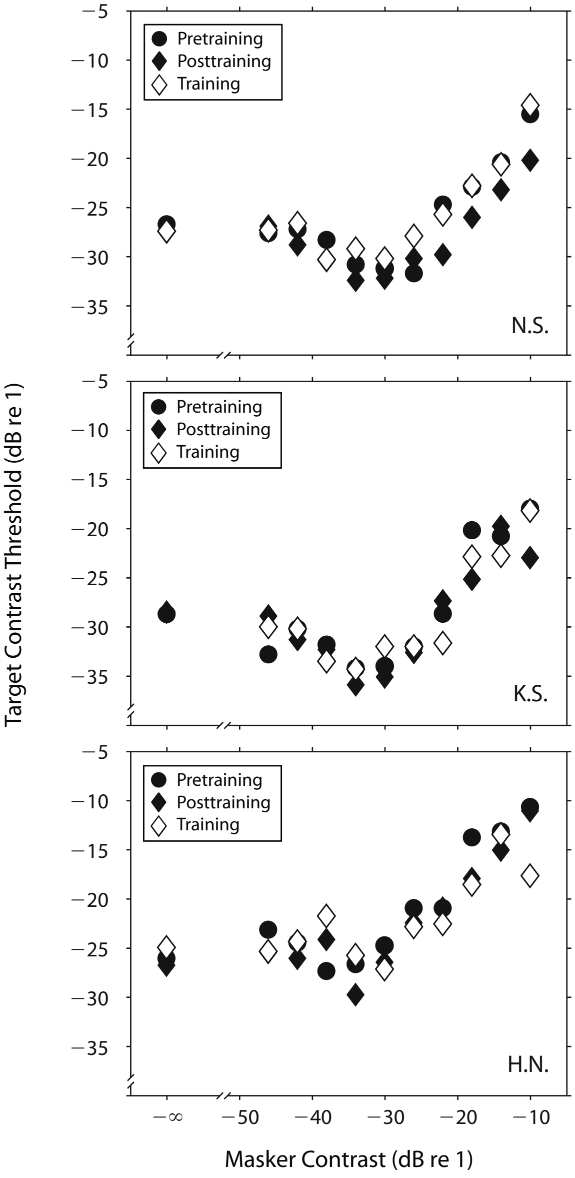

Figure 8. Threshold versus contrast functions for the trained condition after tests for learning transfer.

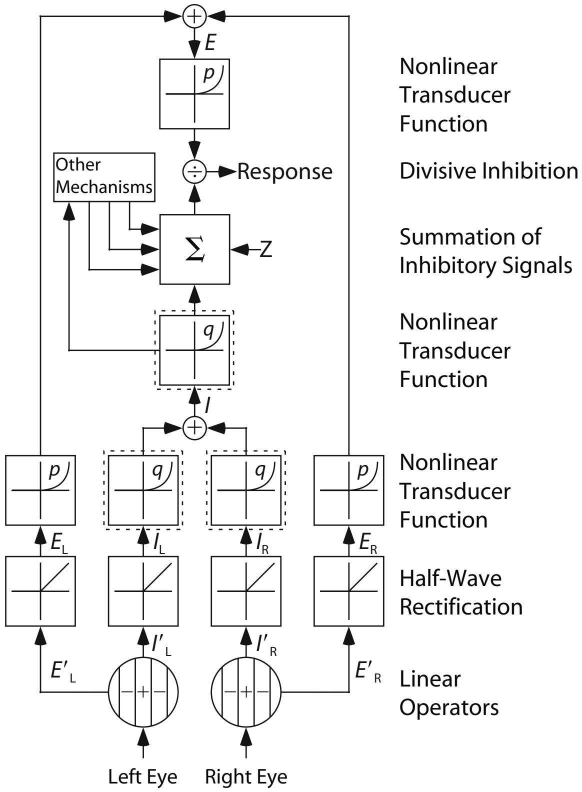

Figure 9. Schematic illustration of the twin summation gain control model. The squares bounded by dashed lines indicate where learning would occur.

where C_{ij} is component contrast and S_{Ei} is the excitatory sensitivity of the mechanism to the normalized luminance profile of component i. Since excitation is a linear process, it is summed across pattern components to yield net excitation E'_j. The equation for monocular excitation produced by the target-plus-masker is the sum of their individual excitations:

$$E'_j = C_{tj}S_{Et} + C_{mj}S_{Em}. \tag{2}$$

Next, the monocular excitations are half-wave rectified:

$$E_j = \max(E'_j, 0). \tag{3}$$

Rectified monocular excitations E_L and E_R originate in the left eye and right eye, respectively. These monocular excitations are raised to power p (subjected to the nonlinear transducer function) and then summed to yield binocular excitation E:

$$E = (E_R)^p + (E_L)^p. \tag{4}$$

The model contains broadband divisive inhibition, which Foley (1994) incorporated in his contrast-processing model. The ideation of divisive inhibition was originally based on the finding that neurons in the visual cortex receive broadband divisive signals, as well as a signal produced by the excitation of cell receptive fields (Heeger, 1992). Inhibitory signals are computed in much the same way excitations are. Monocular inhibitory signals are also products of contrast sensitivity:

$$I'_j = C_{tj}S_{It} + C_{mj}S_{Im}, \tag{5}$$

where S_{Ii} is an inhibitory sensitivity of the mechanism to pattern component i. The monocular inhibitory signals were half-wave rectified, raised to power q, and then summed to yield a binocular inhibitory signal, I.

The mechanism receives binocular inhibitory signals not only from this mechanism, but also from other mechanisms. These binocular inhibitory signals are summed to yield a denominator of divisive inhibition. This summation, however, is omitted from the calculations here, because the targets and maskers in the present study had the same phase, orientation, and spatial frequency.

The binocular excitation and binocular inhibitory signals are raised again to power p or q after the summation of monocular signals. Then, the mechanism response R is computed as the binocular excitation divided by a constant Z, plus the binocular inhibitory signal. These calculations are expressed as

$$R = E^p/(I^q + Z). \tag{6}$$

A target contrast will be the threshold when the response to the target plus masker (R_{t+m}) exceeds the response to the masker alone (R_m) by a constant value. Stated more specifically, behavioral thresholds depend on the value of the decision variable, D:

$$D = R_{t+m} - R_m. \tag{7}$$

At the threshold, $D = 1$.

Simulations of TvC Functions

We simulated TvC functions by adjusting the parameters of the model. The model had seven parameters. Four of the seven parameters represented the sensitivity of linear operators. Excitatory sensitivity to targets S_{Et} was fixed as 100. Excitatory sensitivity to maskers S_{Em}, inhibitory sensitivity to targets S_{It}, and inhibitory sensitivity to maskers S_{Im} were free parameters. Two of the seven parameters were exponents of nonlinear transducer functions: One was an exponent for excitation, p, and the other was an exponent for inhibitory signals, q. The remaining parameter was a semisaturation constant, Z. The TvC functions for monocular masking, as well as those for binocular and dichoptic masking, were simulated.

The smooth curves in Figure 10 correspond to the simulation results of TvC functions with different values of sensitivity to maskers. The middle panel illustrates normal TvC functions that were simulated in our previous study by using the average values of parameters estimated by fitting (Maehara & Goryo, 2005).[4] In comparison with those in the middle panel, the TvC functions in the upper panel are compressed toward the left by an increase in sensitivity to the maskers. In contrast, the TvC functions in the lower panel are stretched rightward. Sensitivity to maskers determines the extent of the effects of masker contrast. Therefore, adjusting sensitivity to the maskers

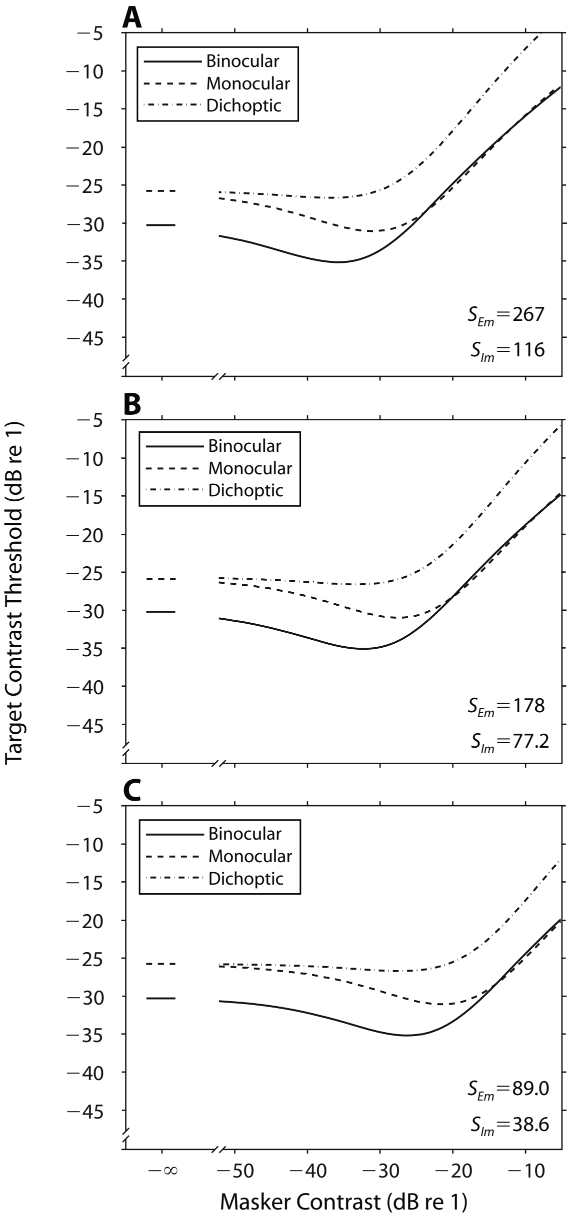

Figure 10. Simulations of threshold versus contrast (TvC) functions with different values of sensitivity for maskers S_{Em} and S_{Im}. (A) TvC functions with increased sensitivity to maskers. (B) Normal TvC functions. (C) TvC functions with decreased sensitivity to maskers.

does not affect the detection thresholds at a masker contrast of −∞ dB.

Figure 11 indicates that a decrease in the exponents of inhibitory signals lowered TvC functions at the higher end of the masker contrast range, and that the width of the downslide was larger for binocular masking. Exponents for inhibitory signals determine the extent to which inhibitory signals are raised in nonlinear transducer functions. Adjusting exponents for inhibitory signals had greater effects at the higher end of the masker contrast range and for binocular masking, because the rise in nonlinear transducer functions grew as values of inhibitions increased. In contrast, adjusting the exponents for the inhibitory signals had little effect on thresholds at the lower end of the masker contrast range—especially at the masker contrast of −∞ dB—because a semisaturation constant mainly determined the denominator of the divisive inhibition.

As was noted above, detection thresholds at the masker contrast of −∞ dB were not changed by adjusting the sensitivity to maskers and were only slightly changed by adjusting exponents of the inhibitory signals. However, simulation results showed that detection thresholds were changed

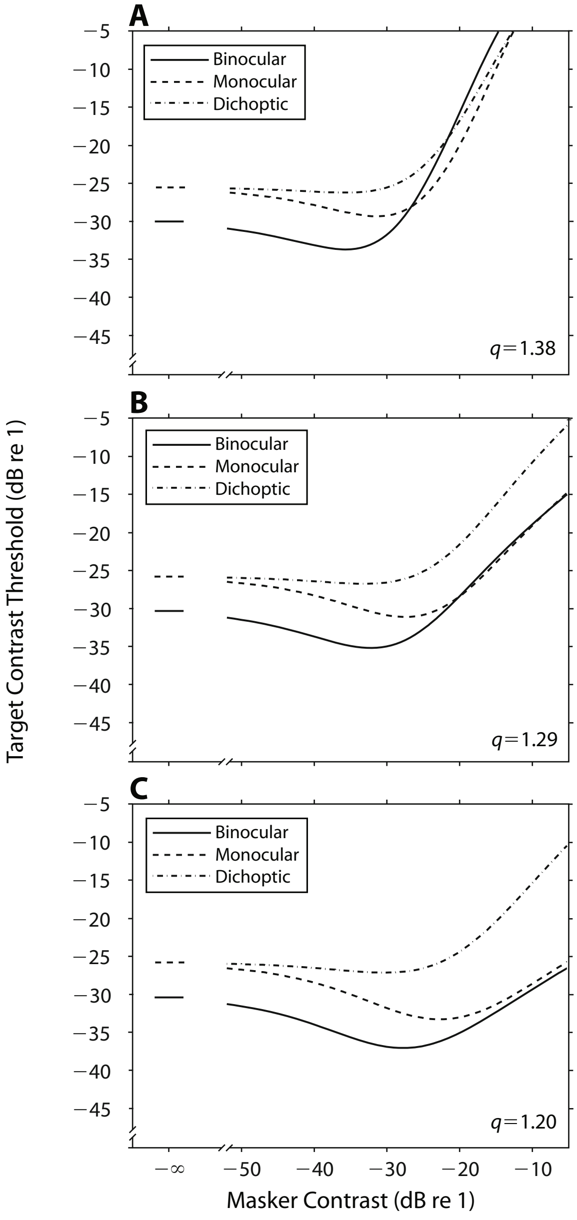

Figure 11. Simulations of threshold versus contrast (TvC) functions with different values of inhibitory-signal exponents, q. (A) TvC functions with increased inhibitory-signal exponents. (B) Normal TvC functions. (C) TvC functions with decreased inhibitory-signal exponents.

by adjusting the inhibitory sensitivity, a semisaturation constant, and exponents for excitation. A decrease in inhibitory sensitivity decreased the values of inhibitory signals, then decreased the denominator of divisive inhibition. The decrease in the denominator lowers the target contrast necessary to produce a decision variable of 1. Therefore, a decrease in inhibitory sensitivity lowers detection thresholds. A decrease in a semisaturation constant also lowers the detection thresholds, because it also causes a decrease in the denominator. The exponents of excitations determine how the excitations are raised in nonlinear transducer functions. When the exponents for excitations increased, the numerator of the divisive inhibition increased, and the denominator decreased relatively. Thus, increasing the exponents for excitations also lowers the detection thresholds.

As was suggested by Experiments 1 and 2, practice did not decrease detection thresholds. Thus, adjustment of the inhibitory sensitivity, a semisaturation constant, or exponents for excitation could not account for the learning in pattern masking. Adjusting these parameters decreased detection thresholds. The next section will address whether learning in pattern masking can be accounted for by adjusting the remaining parameters—namely, sensitivity to maskers and exponents for inhibitory signals.

Model Fitting

Here, we fit the model to the pre- and posttraining data obtained in Experiment 2 using a routine for finding parameter values that minimize the sum of squared error (SSE) between the measurements and the model-predicted values. This routine employs the simplex search method and the "fminsearch" function of MATLAB 6.5. The fitting procedure was as follows. Thirty least-square fits were computed, starting each time with a different set of parameter values randomly sampled from normal distributions estimated in our previous study (Maehara & Goryo, 2005). The recorded fits were those that had achieved the lowest SSE. In fitting to the posttraining data, parameters were varied within ranges centered on parameter means that were estimated by fits in our previous study and extending three standard deviations from those means (Maehara & Goryo, 2005).[5] This step was taken because the number of data points in the present study was small.

First, we fit the model to the posttraining data. The dashed, smooth curves in Figure 3 correspond to the fits. Errors and parameters of the fits are given in Table 1. Except for excitatory sensitivity to targets, the parameters were free parameters that were not fixed in advance. The root mean square errors (RMSEs) were 0.75 dB for N.S., 1.58 dB for K.S., and 1.44 dB for H.N.; fits were reasonably good.

Second, we fit the model to the pretraining data. In this fitting, we set the sensitivity to maskers, exponents for inhibitory signals, or both of these as free parameters, because simulation results suggested that adjustment of these parameters may account for learning. Values for the fixed parameters were set to those of the parameters estimated by fits to the posttraining data. When both the sensitivity to maskers and the exponent for inhibitory signals were set as free parameters (Table 1), RMSEs were 1.20 dB for N.S., 1.48 dB for K.S., and 1.66 dB for H.N. When sensitivity to maskers was set as a free parameter, RMSEs (1.56 dB for N.S., 1.72 dB for K.S., and 1.57 dB for H.N.) were larger than those of the previous fits. When the exponent for inhibitory signals was set as a free parameter, RMSEs (1.19 dB for N.S., 1.49 dB for K.S., and 1.59 dB for H.N.) were comparable to those in the fitting in which both sensitivity to maskers and the exponent for inhibitory signals were set to be free, even though only one parameter was free. This result suggests that learning in pattern masking can be accounted for by decreases in the exponent for inhibitory signals. The solid, smooth curves in Figure 3 correspond to fits to the pretraining data when only the exponent for inhibitory signals was set to be free. In Figure 9, the squares with dashed lines indicate the nonlinear transducer functions for inhibitory signals, where learning would occur.

Table 1
Parameter Values and Errors of Fit Estimated by Fitting the Model to the Data

		Pretraining		
	Posttraining	$S_{Em}+S_{Im}$ + q free	$S_{Em}+S_{Im}$ free	q free
Observer N.S.				
S_{Et}	100.0*	100.0*	100.0*	100.0*
S_{It}	75.1	75.1*	75.1*	75.1*
S_{Em}	171.0	139.0	234.0	171.0*
S_{Im}	116.0	99.4	145.0	116.0*
p	1.44	1.44*	1.44*	1.44*
q	1.25	1.29	1.25*	1.28
Z	17.3	17.3*	17.4*	17.3*
SSE (dB)	6.1	15.7	26.9	15.5
RMSE (dB)	0.75	1.20	1.56	1.19
No. of free parameters	6.0	3.0	2.0	1.0
Observer K.S.				
S_{Et}	100.0*	100.0*	100.0*	100.0*
S_{It}	65.7	65.7*	65.7*	65.7*
S_{Em}	183.0	180.0	268.0	183.0*
S_{Im}	119.0	117.0	171.0	119.0*
p	1.52	1.52*	1.52*	1.52*
q	1.38	1.40	1.38*	1.40
Z	18.4	18.4*	18.4*	18.4*
SSE (dB)	27.6	24.0	32.5	24.5
RMSE (dB)	1.58	1.48	1.72	1.49
No. of free parameters	6.0	3.0	2.0	1.0
Observer H.N.				
S_{Et}	100.0*	100.0*	100.0*	100.0*
S_{It}	75.1	75.1*	75.1*	75.1*
S_{Em}	109.0	45.1	151.0	109.0*
S_{Im}	99.6	52.9	153.0	99.6*
p	1.31	1.31*	1.31*	1.31*
q	1.20	1.26	1.20*	1.22
Z	9.77	9.77*	9.77*	9.77*
SSE (dB)	22.8	30.4	27.2	27.8
RMSE (dB)	1.44	1.66	1.57	1.59
No. of free parameters	6.0	3.0	2.0	1.0

*Fixed parameters.

Consider now the function of the learning accounted for by the decrease in the exponent for inhibitory signals. Figure 12 shows input–output functions with different values of exponents for inhibitory signals. The *x*-axis represents the contrast of input stimuli. The *y*-axis represents the mechanism response. In simulations of input–output functions, parameters were set as average values estimated by fits to the posttraining data, except for exponents for inhibitory signals. Curves at the starting point of the arrows represent functions with inhibitory-signal exponents of 1.31. Curves at the end points of the arrows represent functions with inhibitory-signal exponents of 1.29. As is indicated in Figure 12, the slopes of the curves become steeper at the higher end of the input range when the exponents for the inhibitory signals are lower; that is, changes in response, which were caused by changes of the input, became larger with decreases in the inhibitory-signal exponents. This means that mechanisms became more sensitive to changes in contrast at the higher end of the masker contrast range. However, functions with different inhibitory-signal exponent values almost overlapped at the lower end of the input range. This finding is consistent with results that showed little practice effect at the lower end of the masker contrast range.

Although the RMSEs were small enough to indicate reasonable fits, the fits for H.N. did not show a decrease in thresholds at the lower end of the masker contrast range, whereas fits for the other observers had a dipper shape. The thresholds for H.N. were higher at masker contrasts of -46 to -38 than were those at the masker contrast of $-\infty$. Fitting errors for H.N. were actually larger at the lower end of the masker contrast range. The performance of H.N. may have been affected by mechanisms other than those included in our model.

GENERAL DISCUSSION

The results of this study show that practice decreased contrast thresholds when maskers were presented. The threshold decrease tended to be larger at the higher end of the masker contrast range. Learning did not occur when maskers were not presented. Learning partly transferred to conditions in which the stimuli phases were changed by 180º. The extent of learning transfer was different among observers when the stimuli orientation was changed and when stimuli were presented to the untrained eye. We simulated changes in TvC functions using our contrast processing model and fit the model to the pre- and posttraining data. Simulation results and model fit showed that learning in pattern masking can be accounted for by the decrease in inhibitory-signal exponents. Such learning may reflect the visual system's becoming more sensitive to changes in contrast.

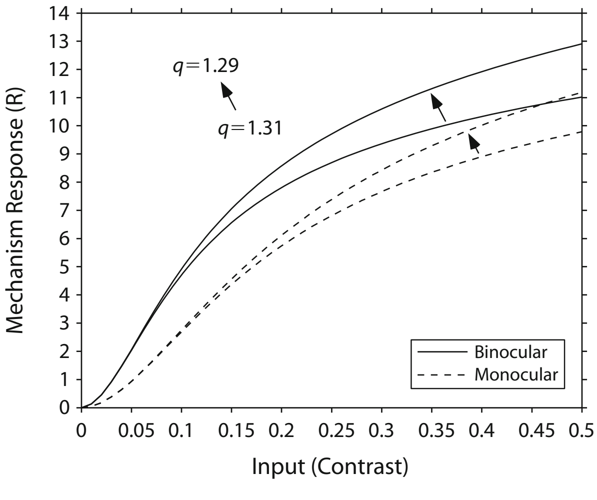

Figure 12. Changes in input–output functions with decreased inhibitory-signal exponents. Contrasts are expressed as Michelson contrasts. Slopes of functions become steeper with a decrease in the inhibitory-signal exponents.

The learning transfer to stimuli with the untrained phase suggests that learning occurs at processing levels when different phases are processed together, although the model calculations in the present study were limited to the processing of only one type of phase. However, we assumed that inhibitory signals were pooled over mechanisms (Figure 9) tuned to different phases, orientations, and spatial frequencies. Given that inhibitory signals from different mechanisms were raised to the same power, our model's predictions are consistent with findings showing that learning transferred to the untrained phase.

The extent of interocular transfer in the present study differed among observers. Yu et al. (2004) also reported that 2 out of 3 observers showed interocular transfer. The interocular transfer of learning suggests that changes in processing after the summation of monocular signals may result in learning. For modeling simplicity, we assumed that inhibitory signals were raised to the power *q* twice before and after the summation of monocular signals; but exponents were probably different between the first and the second nonlinear transducer functions. Georgeson and Meese (2005) recently suggested that, near threshold, the first excitatory transducer functions were nearly linear, whereas the second transducer functions had quadratic nonlinearity. We plan future research, therefore, on learning in dichoptic pattern masking. If we fit the model to data in monocular and dichoptic masking conditions, we should be able to further specify where learning occurs.

Yu et al., (2004) noted that changes in contrast gain control mechanisms cannot account for learning, because such mechanisms cannot explain the specificity of learning to a masker contrast. Although this may be the case, their results (Yu et al., 2004, Figure 3C) showed that learning was partly transferred to the untrained masker contrasts. Therefore, it is possible that changes in contrast gain control mechanisms also contribute to learning in pattern masking.

In the present study, we presented a Gabor target on a larger grating masker. Our stimuli were similar to those used by Adini et. al (2002), in that maskers were presented not only on the target location, but also on spatial regions adjacent to a target. The present results are consistent with their results, in which they found that learning occurred at the higher end of the masker contrast range, but not at the lower end of the masker contrast range. However, slopes of TvC functions at the high end of the masker contrast range were less steep for their results than they were for the present results. According to Adini et al.'s (2002) Figure 2, there were but small differences among thresholds at masker contrasts of about −16 dB to −12 dB (13%–25%). On the other hand, Swift and Smith (1983) reported that the slope of TvC functions was initially 1 and decreased to 0.65 with practice. These values are comparable to those of 2 out of 3 observers in the present study, although Swift and Smith's experiment differed from ours in stimuli and training duration. TvC function slopes did not change with practice when targets and maskers were equal in size (Yu et al., 2004). It would be reasonable to suppose that stimuli presented on the adjacent regions effect change in the slopes of TvC functions.

Our model assumes different sensitivities for the target and masker. These sensitivities may have to be equal if they are to activate the same receptive field. However, fits to the data show larger differences between the target and masker sensitivities (Table 1). Polat and Sagi (1993) suggested the presence of suppressive and facilitatory lateral interactions between mechanisms for which receptive fields are close to each other. Although our model does not incorporate lateral interaction, we suspect that differences in sensitivities would reflect effects from regions around the target location.

Using their model, Adini et al. (2002) simulated changes in TvC functions. Response was determined by a recurrent mutual network between the excitatory and the inhibitory subpopulations. The inhibitory subpopulation mainly received lateral inputs evoked by the presentation of flanking maskers. According to their model simulations, learning in lateral masking reflected modifications in connection with the two subpopulations. Using our model to evaluate the effects of flanking maskers is problematic, because lateral interactions were not modeled. However, Yu et al. (2004) reported that thresholds also decreased with practice when flanking maskers were not presented. This result cannot be explained with Adini et al.'s (2002) model. Whether learning in pattern masking is associated with either or both of these mechanisms remains in question.

One might argue that there are models other than ours that could account for perceptual learning in pattern masking. Adini et al. (2002) explained it by changes in lateral interaction. Yu et al. (2004) assumed that practice narrows the dynamic range of one of multiple contrast-selective mechanisms; the decision stage "learns" to attend to output from the mechanism most sensitive to a range of stimulus contrast. Swift and Smith (1983) argued that observers would learn to use particular local criteria for making any given distinction. Moreover, Dosher and Lu (1999) proposed a perceptual template model that can account for perceptual learning in various tasks. Their perceptual template model assumes that practice could decrease three types of noise: internal additive noise, external noise, and multiplicative internal noise. It would be beyond the scope of this article to discuss whether these models are correct. Some mechanisms might work together. However, the models above do not assume changes in nonlinear transducer functions for divisive inhibitory signals. We propose that such changes could cause perceptual learning.

Conclusion

The present study suggests that changes in nonlinear transducer functions for divisive inhibitory signals affect learning in pattern masking. With this learning mechanism, the visual system becomes more sensitive to changes in contrast. Divisive inhibition has been incorporated into models for various tasks, including motion detection (Georgeson & Scott-Samuel, 1999) and stereopsis (Read & Cumming, 2004). Thus, learning in pattern masking and learning in various tasks may both be accounted for by changes in nonlinear transducer functions for divisive inhibitory signals.

AUTHOR NOTE

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NOTES

1. This means that contrast of a Gabor target changes.

2. We also tested equality of the slopes for each observer. There were no significant difference in slope between pre- and posttraining (p = .125 for N.S., .454 for K.S., and .964 for H.N.). However, the sample size (five masker contrasts) might be too small to detect the difference in slope.

3. For dichoptic masking, targets were presented to one eye, while maskers were presented to the other eye.

4. The parameter means determined by our previous study are as follows: $\overline{S}_{Et} = 100$ (Fixed); $\overline{S}_{It} = 37.9$; $\overline{S}_{Em} = 177.9$; $\overline{S}_{Im} = 77.2$; $\overline{p} = 1.38$; $\overline{q} = 1.29$; and $\overline{Z} = 20.3$. We used these means as the parameter values for the simulation of normal TvC functions. The normal TvC functions are plotted in Figures 10 and 11.

5. The standard deviations of parameters as determined by our previous study were as follows: $\sigma(\overline{S}_{It}) = 12.4$; $\sigma(\overline{S}_{Em}) = 23.1$; $\sigma(\overline{S}_{Im}) = 13.9$; $\sigma(\overline{p}) = 0.049$; $\sigma(\overline{q}) = 0.031$; $\sigma(\overline{Z}) = 10.9$.

APPENDIX
Summary of Symbols

S_{Ei}	excitatory sensitivity parameters to pattern component i
S_{Ii}	inhibitory sensitivity parameters to pattern component i
p	exponents for excitations
q	exponents for inhibitory signals
Z	semisaturation constants
C_{ij}	Michelson contrast of pattern component i presented to eye j
E'_j	monocular excitations by pattern presented to eye j
E_j	half-wave rectified monocular excitations by pattern presented to eye j
E	binocular excitations
I'_j	monocular inhibitory signals by pattern presented to eye j
I_j	half-wave rectified monocular inhibitory signals by pattern presented to eye j
I	binocular inhibitory signals
R	mechanism responses
D	the decision variable at threshold $D = 1$

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