

Exogenous and endogenous attention during perceptual learning differentially affect post-training target thresholds

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There is conflicting evidence in the literature regarding the role played by attention in perceptual learning. To further examine this issue, we independently manipulated exogenous and endogenous attention and measured the rate of perceptual learning of oriented Gabor patches presented in different quadrants of the visual field. In this way, we could track learning at attended, divided-attended, and unattended locations. We also measured contrast thresholds of the Gabor patches before and after training. Our results showed that, for both exogenous and endogenous attention, accuracy in performing the orientation discrimination improved to a greater extent at attended than at unattended locations. Importantly, however, only exogenous attention resulted in improved contrast thresholds. These findings suggest that both exogenous and endogenous attention facilitate perceptual learning, but that these two types of attention may be mediated by different neural mechanisms.

Keywords: perceptual learning, exogenous attention, endogenous attention, contrast threshold, Gabor patch

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Introduction

Information processing of visual stimuli improves with repeated experience with those stimuli (e.g., Ahissar & Hochstein, 1997; Karni & Sagi, 1991; Watanabe et al., 2002). Such perceptual learning is an important ability because it enables us to respond more efficiently to environmental cues. Given the specificity of perceptual learning to the trained retinotopic location (Fahle, Edelman, & Poggio, 1995; Schoups, Vogels, & Orban, 1995; Shiu & Pashler, 1992), stimulus size (Ahissar & Hochstein, 1996), stimulus orientation (Ahissar & Hochstein, 1997; Fiorentini & Berardi, 1981; Ramachandran & Braddick, 1973), direction of motion (Ball & Sekuler, 1987; Watanabe, Nanez, & Sasaki, 2001), and the eye used during training (Karni & Sagi, 1991), it is not surprising that both human

brain imaging and monkey electrophysiological recording studies have attributed the underlying neural mechanism to plastic changes in early visual areas (Fahle, 2004; Ghose, 2004; Gilbert, Sigman, & Crist, 2001; Karni, 1996).

Repeated experience with a visual stimulus does not, however, guarantee improvements in behavior. Several studies have reported considerable intersubject variability in both the occurrence and magnitude of perceptual learning (Fahle et al., 1995; Fahle & Henke-Fahle, 1996; Mukai et al., 2007; Schmitt, Kromeier, Bach, & Kommerell, 2002). Attention has been implicated in both psychophysical and electrophysiological studies as playing a key role in explaining this variability (Ahissar & Hochstein, 1993; Crist, Li, & Gilbert, 2001; Fahle, 2004; Li, Piech, & Gilbert, 2004; Shiu & Pashler, 1992). For example, Ahissar and Hochstein (1993) showed that when subjects are exposed to a visual stimulus, learning occurs for the

task-relevant (i.e., attended) but not for the task-irrelevant (i.e., unattended) stimulus features. Additional support for the idea that attention plays a key role in perceptual learning comes from our prior neuroimaging study (Mukai et al., 2007), in which we found that subjects who subsequently learned the task had greater initial brain activation in cortical areas associated with the attentional network (i.e., parietal and prefrontal regions) than subjects who did not subsequently learn. Additionally, we found that the brain activation in those attention-related regions negatively correlated with the improvements in performance during training.

Another line of evidence indicates, however, that attention does not play an important role in perceptual learning (Nishina, Seitz, Kawato, & Watanabe, 2007; Seitz & Watanabe, 2003; Watanabe et al., 2002, 2001). One particularly striking example comes from a study by Watanabe et al. (2001) who found that perceptual learning can occur when the stimuli are task-irrelevant, therefore unattended, and the stimuli are presented at a subthreshold level.

The present study was therefore undertaken to directly assess the effects of attention on perceptual learning by contrasting attended, divided-attended, and unattended conditions. We were able to contrast the effects of these three levels of attention in the same subjects because perceptual learning is known to be location specific (Fahle et al., 1995; Schoups et al., 1995; Shiu & Pashler, 1992). Hence, we designated one stimulus location (one visual field quadrant) as attended, two other locations (two other visual field quadrants) as divided-attended, and the last location (the fourth quadrant) as unattended, and we compared behavioral improvements in performance at each of the different stimulus locations. During training on the task, a discrimination of oriented Gabor patches, we monitored changes in response accuracy and reaction time (RT), and we also measured contrast thresholds before and after training at each stimulus location. Finally, we manipulated the type of spatial attention by presenting either exogenous attentional cues (briefly flashed boxes) or endogenous attentional cues (pointing arrows or colored boxes that matched the color of a central cue) to different groups of subjects. Whereas exogenous attention is a stimulus-driven, involuntary, and transient type of attention, endogenous attention is a goal-driven, voluntary, and sustained type of attention (Egeth & Yantis, 1997), and thus we hypothesized that the effects of these two types of attention on perceptual learning might differ.

Methods

Study design

To test the hypothesis that attention is important in facilitating perceptual learning, we had subjects allocate three different *levels of attention* (attended, divided-

attended, and unattended) to different stimulus locations during training with low-contrast oriented Gabor patches (sine gratings enveloped by a Gaussian). We compared contrast thresholds at each location, measured before and after training, to assess whether different degrees of improvement in threshold occurred at the four different locations (i.e., for different levels of attention). We also monitored changes in response accuracy (percent correct) and RT during training and compared the changes among the different locations, again to assess improvements in performance for the different levels of attention. To examine possible differential effects of two different *types of attention* (exogenous and endogenous attention) on perceptual learning, we trained one group of subjects with an exogenous attentional cue and two groups of subjects with different types of endogenous attentional cues. For the exogenous attentional cue, we adapted a paradigm developed by Yantis and Jonides (1984) and presented a visually salient cue (white square-shaped frame) abruptly at one (attended) or two (divided-attended) of the four stimulus locations (located eccentrically in the visual field); these abrupt salient cue(s) drew attention exogenously. The remaining visual quadrant served as the unattended location. For one of the endogenous attentional cues, we adapted a paradigm developed by Posner (1980) and Posner, Cohen, and Rafal (1982) and presented an arrow at the center of the visual field, pointing at one (attended) or two (divided-attended) of the four stimulus locations. For the other endogenous attentional cue, we modified a paradigm employed by Rossi, Bichot, Desimone, and Ungerleider (2007) and presented four colored square-shaped frames (green, red, blue, and yellow) at the four stimulus locations (located eccentrically in the visual field), such that one (or two) of the frame(s) had colors that matched the color of the central fixation spot, indicating the location(s) to be attended. We employed this second endogenous attentional cue task to better match the location of the exogenous and endogenous attentional cues relative to the location of the target stimulus. That is, the colored endogenous frames were located in the same positions in the visual field as the flashed exogenous white frame(s). The detailed procedures we employed to manipulate spatial attention during training are described in the [Stimuli and task](#) section below. To summarize the design, we had two independent variables, i.e., level of attention and type of attention. There were three levels of attention: attended, divided-attended, and unattended. There were three attentional cues: one exogenous cue and two endogenous cues (pointing arrow and colored frames); separate groups of subjects were trained on the three different attentional cues.

Subjects

Thirty-six normal volunteers completed the experiment (13 males, 23 females). All subjects provided informed

consent prior to the experiment, and none had participated in any perceptual learning study before the current one. All procedures were approved by the NIMH Institutional Review Board. All subjects had normal or corrected-to-normal vision. Each subject was randomly assigned to one of the three attentional cue groups: exogenous, endogenous/arrow cue, or endogenous/color cue. Those groups consisted of 12 subjects: 6 males and 6 females (mean age 27 ± 5), 2 males and 10 females (mean age 25 ± 3), and 5 males and 7 females (mean age 25 ± 5) for the exogenous, endogenous/arrow cue, and endogenous/color cue groups, respectively.

Apparatus

In a dimly lit room, stimuli were presented on a 19-inch liquid crystal display monitor with a resolution of 1280×1024 pixels and a refresh rate of 60 Hz. The gray level of the stimulus background was set at the average of the highest and lowest luminance levels of the monitor (i.e., at 39.5 Lux). We did gamma correction on the monitor using Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). The monitor was placed 57 cm away from the subject's eyes, and we used a chin rest to minimize the subject's head motion. To generate stimuli, we used MATLAB 7.4 (Mathworks, Massachusetts) and Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). To ensure that the subjects fixated the center of the stimulus display during the experiment, we monitored the subject's gaze position using a video-based eye-tracking system with remote pan tilt optics (Model 504, Applied Science Laboratory, Massachusetts).

Stimuli and task

We used a Gabor patch as the test stimulus for measuring contrast thresholds at each of four stimulus locations before and after training. Gabor patches were also used as the stimuli during training. During the contrast threshold trials, we presented one Gabor patch at a time at each of the four locations, and the contrast of the Gabor patch was increased/decreased based on the subject's response. On the other hand, during the training trials, we presented Gabor patches at four stimulus locations simultaneously and the contrast of Gabor patches was held constant at the level at which $\sim 75\%$ correct responses were obtained for that subject during the threshold measurement prior to the training. A fixation spot was presented in the middle of the screen at all times during the experiment to allow subjects to maintain their gaze position at the central fixation. The size of a Gabor patch was 2×2 degrees in visual angle, located 3 degrees from central fixation. Each Gabor patch was oriented either 45 degrees or 135 degrees from the vertical. A detailed configuration of the test and training stimuli is shown in Figure 1. For both the contrast threshold

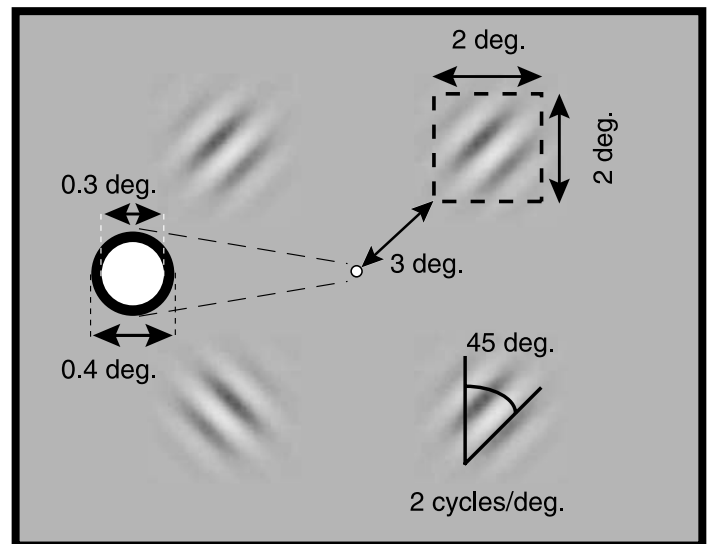


Figure 1. An example of the Gabor patch stimuli (sine-wave gratings enveloped by Gaussian) used in the experiment. The sine-wave grating's angular frequency was two cycles per degree. There were four stimulus locations, and each Gabor patch was presented in a 2×2 degree squared area (depicted by the dashed rectangle, which was not shown during the experiment). The contrast of the Gabor patches during training was set at each subject's contrast threshold of $\sim 75\%$ correct level measured pre-training. The fixation spot was white and outlined by a black contour.

measurements and training trials, the subject's task was a two-alternative forced-choice (2AFC) decision to indicate whether the Gabor patch was rotated clockwise or counterclockwise relative to the vertical.

The experiment consisted of three parts, totaling six sessions (Figure 2): (1) a contrast threshold measurement in the first session, prior to training; (2) four sessions (2560 total trials) of training on Gabor patches with attentional cues; and (3) a second contrast threshold measurement in the sixth session, after training. Each session was conducted on a separate day, and the experimental environment was constant throughout.

To measure contrast thresholds, we used the staircase method (e.g., Cornsweet, 1962; Gracely, Lota, Walter, & Dubner, 1988). On each trial, a fixation spot was presented for 50 ms, followed by a 50-ms presentation of a single Gabor patch. Next, subjects were prompted by a color change of the central fixation circle to perform the 2AFC task on the orientation of the Gabor patch by pressing one of two buttons on a response device; one button indicated that the Gabor patch was oriented clockwise from vertical and the other button indicated that the patch was oriented counterclockwise from vertical. The response period was set unlimited to encourage subjects to commit to doing the task instead of just pressing buttons as quickly as possible. Once the subjects pressed a button, the next trial began. During the

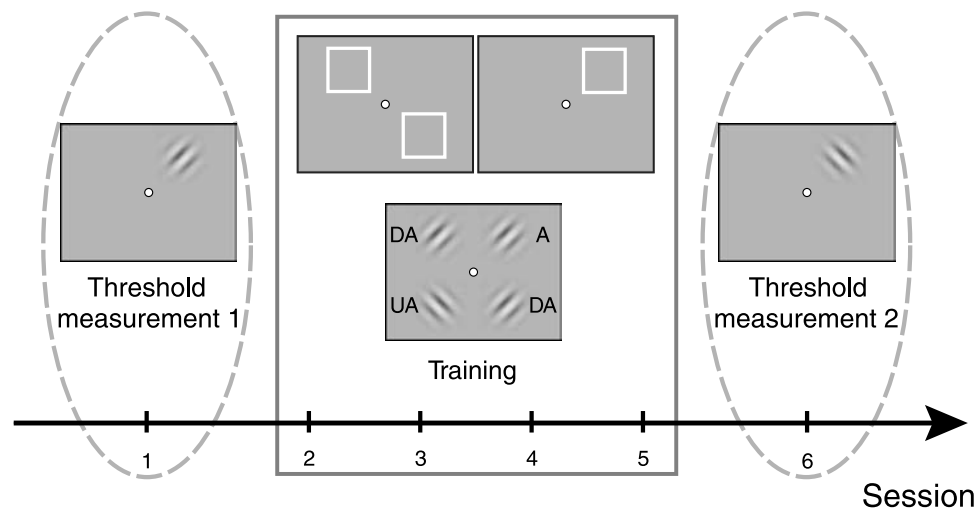


Figure 2. The time course of the experiment. During the first and last sessions, we measured each subject's contrast threshold of $\sim 75\%$ correct at each of four stimulus locations. During sessions 2 through 5, subjects were trained on an orientation discrimination task at these four locations. We manipulated attention during training by using attentional cues (in this example, exogenous attentional cues) at the four stimulus locations. There were three levels of attention: attended (A), divided-attended (DA), and unattended (UA).

threshold measurements, no attentional cues were presented at any location. The contrast of the Gabor patch was reduced 1% after a subject responded correctly three times in a row and was increased 1% when a subject responded incorrectly once, thus yielding an accuracy of $\sim 75\%$ correct. We measured contrast thresholds twice at each of the four locations, once starting with a high contrast of 10% and once starting with a low contrast of 1%. Each staircase ended after ten reversals and we averaged the values for the total of 20 reversals; the order of locations tested was randomized among the subjects.

For the training sessions, on each trial, the attentional cue(s) preceded the simultaneous presentation of four Gabor patches, one in each quadrant of the visual field. To have three different levels of attention at the different stimulus locations, we presented one attentional cue in one-half of the training trials and two attentional cues in the other half. The location(s) to which attention was directed by one or two cues were defined as the attended and divided-attended locations, respectively (Lu & Doshier, 1998). The location to which attention was not directed by any attentional cue during training was defined as the unattended location. The attended and unattended locations were always placed diagonally (e.g., visual field quadrants I and III), and the two remaining locations were the divided-attended locations (e.g., quadrants II and IV; see Figures 2 and 3). These locations were randomly assigned to each subject and counterbalanced among the subjects.

We used the following three types of attentional cues during training: (1) exogenous cue, which was a white square-shaped frame presented at one (or two) stimulus location(s) for 67 ms (Figure 3a). This abrupt and salient cue was used to attract the subject's attention automatically (e.g., Carrasco, Ling, & Read, 2004). The subjects

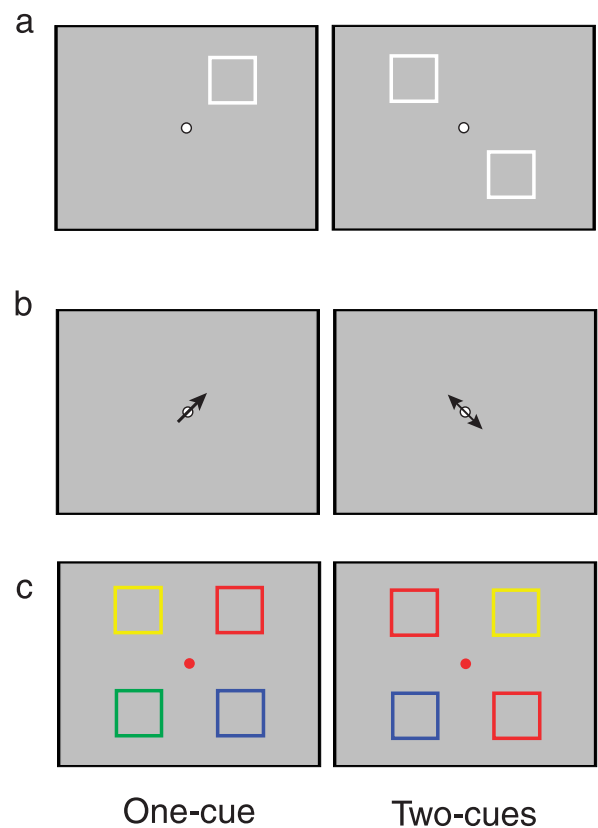


Figure 3. Attentional cues used during training. (a) Exogenous cues were presented for 67 ms. (b) Endogenous arrow cues were presented for 300 ms. (c) Endogenous color cues were presented for 300 ms. In this example, the stimulus location in quadrant I is cued by "One cue," and the stimulus locations in quadrants II and IV are cued by "Two cues"; hence, these locations are attended and divided-attended, respectively. The remaining stimulus location in quadrant III is unattended.

were told that the white frame(s) were not related to the task. (2) Endogenous/arrow cue, which was a black arrow presented in a 2×2 degree square area at the center of the visual field for 300 ms (Figure 3b). The arrow(s) pointed at one stimulus location or at two locations diagonally opposite each other, and subjects were instructed to shift their attention from fixation to the direction(s) where the arrow(s) pointed. (3) Endogenous/color cue, which consisted of four colored square-shaped frames (green, red, blue, and yellow), was presented simultaneously in the four stimulus locations for 300 ms (Figure 3c). Prior to the appearance of the four colored frames, the central fixation spot's color changed, and subjects were instructed to shift

their attention from fixation to the location(s) where the frame(s) matched the color of the central fixation spot. The size and location of the colored frames in this third condition matched the size and location of the white frame(s) used for the exogenous attention condition. The presentation durations of the attentional cues were chosen so that the effects of exogenous and endogenous attention would be maximized (Carrasco et al., 2004; Cheal & Lyon, 1991; Muller & Rabbitt, 1989; Nakayama & Mackeben, 1989).

The time course of a training trial for exogenous and endogenous attention is shown in Figure 4. In each trial, either one or two attention cues was followed by the presentation of the training stimuli (Gabor patches). Then,

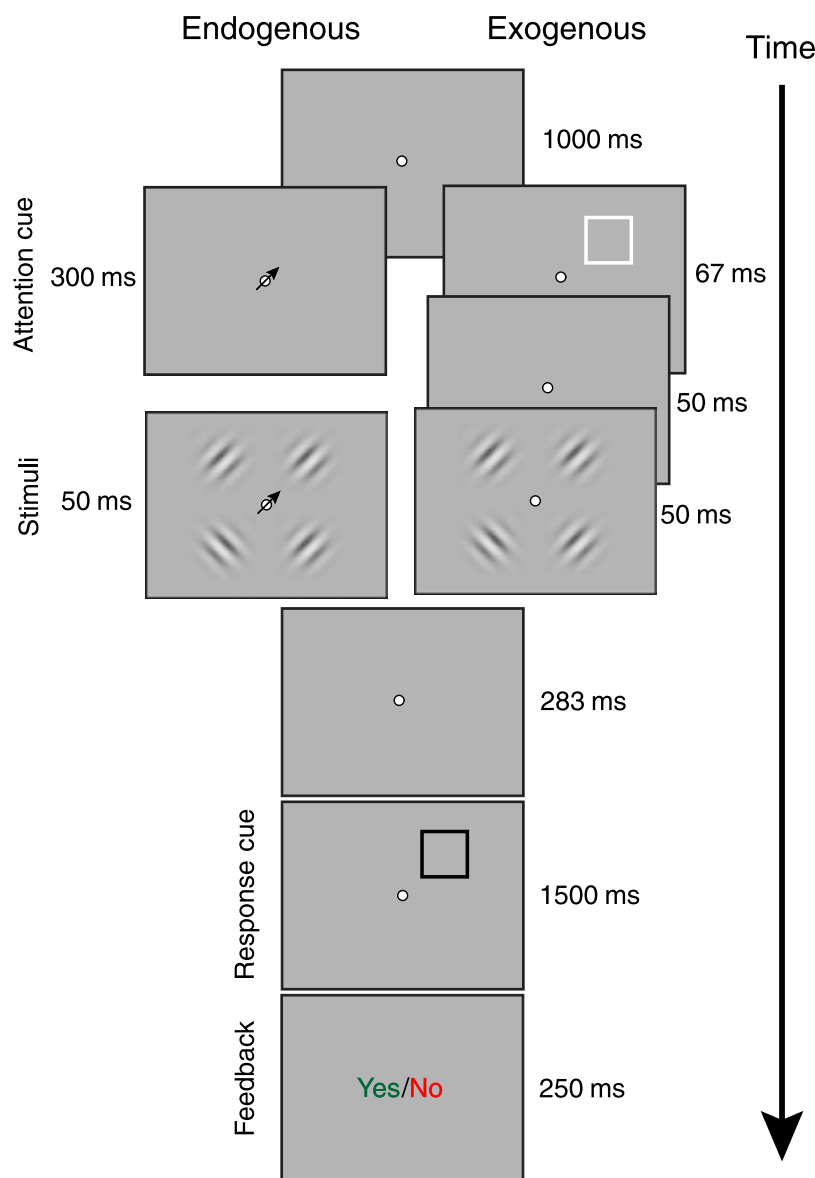


Figure 4. A sample time course of a training trial. Endogenous color cue's time course was the same as the endogenous arrow cue, which is depicted here. In valid trials, the attentional cue(s) and response cue were presented at the same location(s), as shown here. In invalid trials, the response cue was presented at a different location from where the attentional cue(s) appeared. During the feedback period, "YES" in green was presented when the response was correct, "NO" in red was presented when the response was incorrect, and "NO RESPONSE" in blue was presented when the subject did not make a button response during the response period.

a response cue, which was a black square-shaped frame, appeared at one of the four training stimulus locations. The subjects were instructed to perform the 2AFC task on the orientation of the Gabor patch presented at the location where the response cue appeared. The response period was set constant (1500 ms) during training to ensure constant trial length. After the response period, subjects received feedback based on their response. The subject's response (correct/incorrect) and RT data were recorded for each trial to assess the changes in performance during training. For exogenous attentional trials, the response cue appeared at equal probability in all the locations. Thus, the stimuli at all the four locations were equally task relevant. One attentional cue was valid 25% of the time, and two attentional cues combined were valid 50% of the time. In other words, the attentional cues did not predict the task location (Jonides, 1981). For endogenous attentional trials, the attentional cues were valid 70% of the time. We raised the proportion of valid trials for the endogenous attentional trials to encourage subjects to shift their attention according to the attentional cues (Yantis & Jonides, 1990).

Data analyses

First, we ran a two-way (four stimulus locations \times three attentional cue groups) mixed-design ANOVA on the contrast threshold data from the session prior to training to ensure that contrast thresholds at the four stimulus locations were properly matched and did not differ among subjects assigned to different attentional cue groups.

For the rest of the analyses, we combined the data from the two divided-attended locations by averaging them, because we did not find any significant difference between them in each attentional cue group. The procedures for comparing the data between the two divided-attended locations for different analysis and the results are described in [Supplementary materials](#).

To confirm that the subjects' attention was allocated to the cued location(s) during training as we intended, we assessed attentional effects on the subjects' performance before they started learning. Accordingly, we ran a two-way (three levels of attention \times three attentional cue groups) mixed-design ANOVA on the percent correct and averaged RT data from the first 30 trials (early training period). For this analysis, we used the data only from the early training period to minimize the subsequent effect of perceptual learning. For the attended and divided-attended attention conditions, we used the data from valid-cue trials only. Following ANOVAs, we ran paired *t*-tests to determine the levels of attention that showed significant differences from each other in accuracy and/or RT during the early period of training.

To determine if there were improvements in accuracy and/or RT during training, we ran a linear regression analysis on the averaged time-course data for each level of

attention for each attentional cue group, and we tested whether the slope of each learning curve's fit to the time-course data was significantly different from zero. After the regression analysis, we also tested regression slope homogeneity to determine whether the slopes of the learning curves for the three different levels of attention in each attentional cue group differed from each other. For both the accuracy (percent correct) and RT data, we calculated the mean of each time point by averaging the data for every 10 trials. In this analysis, we again used the data from valid trials only for the attended and divided-attended level of attention conditions. We had different numbers of trials for different level of attention conditions in the endogenous paradigms, because there was a greater proportion of valid-cue trials for the attended and divided-attended conditions. Therefore, to equate the number of trials across all the levels of attention in the exogenous and endogenous cue groups, for each attention level and type of attentional cue, we analyzed the accuracy data from the first 320 trials, which was the minimum number of trials of data we collected. Similarly, for the RT data, we included only the correct trials from the first 320 trials.

Prior to comparing the effect of exogenous and endogenous types of attention on the improvement in contrast threshold, we compared the data from the two endogenous attentional cue paradigms by running a three-way (three levels of attention \times pre- vs. post-training sessions \times two endogenous attentional cue paradigms) ANOVA. Because we found no significant main or interaction effects between the two endogenous attentional cue (arrow and color) paradigms, we combined the data from both for the rest of the analyses. To examine the effect of attention and the differential effects of exogenous and endogenous attention on improvements in contrast threshold, we ran a three-way (three levels of attention \times pre- vs. post-training sessions \times two types of attention) ANOVA. Following ANOVAs, we ran paired *t*-tests to determine the levels and types of attention in which perceptual learning occurred.

To assess the relationship between performance changes during training and changes in contrast thresholds measured before and after training, we ran correlational analyses on the detected changes in percent correct/RT and contrast thresholds across the subjects for each level and type of attention condition. The changes in percent correct and RT were calculated by subtracting the averaged performance during the first quarter of the training period from the last quarter of the training period.

For the eye position data, we first defined four areas of interest: the area around the central fixation, the attended stimulus location, the divided-attended stimulus locations, and the unattended stimulus location. Then, we calculated the percentage of duration each subject's gaze fell in each area of interest and averaged the data for each type of attention. To confirm that subjects fixated at the central fixation area during the experiment and that the gaze durations at the different stimulus locations did not differ

for the different types of attention, we ran a four (area of interest) \times two (type of attention) ANOVA on the gaze duration data.

Results

Contrast thresholds before training

For contrast thresholds before training (Figure 6), a four (stimulus location) \times three (attentional cue group) mixed-design ANOVA showed that the main effects of neither stimulus location nor attentional cue group was significant ($F[3,99] = 0.330$, $p = 0.804$; $F[2,33] = 0.055$, $p = 0.946$, respectively). The interaction effect between stimulus location and attentional cue group was also not significant ($F[6,99] = 0.424$, $p = 0.861$). Therefore, prior to training, contrast thresholds of the Gabor patches were at the same level at all the stimulus locations for all the subjects, irrespective of the subjects' assignment to different attentional cue groups.

Manipulation of attention during training

To confirm that our attention manipulation worked, we compared the response accuracy (percent correct) and RT during the early period of training (i.e., the first 30 trials), before perceptual learning had an impact on performance for the different levels of attention (i.e., attended, divided-attended, and unattended). The mean accuracy and RT, respectively, for all the attentional cue groups averaged together were 68% and 718 ms at attended, 61% and 765 ms at divided-attended, and 53% and 826 ms at unattended locations. A three (level of attention) \times three (attentional cue group) mixed-design ANOVA revealed that for both accuracy and RT the main effect of level of attention was significant ($p < 0.001$), whereas the main effect of attentional cue group ($p = 0.548$ for accuracy, $p = 0.113$ for RT) and the interaction effect of level of attention by attentional cue group ($p = 0.497$ for accuracy, $p = 0.812$ for RT) were not. The results of t -tests following the ANOVA showed that the averaged accuracy level across the attentional cue groups at the attended location was higher than at both the divided-attended ($p = 0.005$) and unattended locations ($p = 5.2 \times 10^{-7}$) and was higher at divided-attended locations than at the unattended location ($p = 6.6 \times 10^{-5}$). Furthermore, the RT was shorter at the attended location than at both the divided-attended ($p = 0.001$) and unattended locations ($p = 2.9 \times 10^{-4}$) and was also shorter at the divided-attended locations than at the unattended location ($p = 0.005$). Therefore, during this early training period, all exogenous and endogenous attentional cues were successful in having subjects allocate their attention to the cued locations.

Behavioral changes during training

Figure 5 shows the behavioral changes in accuracy and RT during training for the subject groups trained with the exogenous and endogenous attentional cues. The slopes of the learning curves for accuracy are summarized in Table 1.

For all attentional cues, the slopes of the learning curves for accuracy at the attended and divided-attended locations were significantly greater than zero ($p < 0.05$). On the other hand, the slopes of the learning curves at the unattended location were not different from zero in either of the groups trained with endogenous cues ($p = 0.18$ and $p = 0.95$ for the arrow cue and color cue, respectively), although the slope was significantly greater than zero at the unattended location for the group trained with exogenous cues ($p = 4.1 \times 10^{-4}$). Thus, accuracy improved at attended and divided-attended locations for all subjects, irrespective of the attentional cue, but no improvement was found at the unattended location for the groups trained with endogenous attentional cues.

An analysis of regression slope homogeneity showed that, for accuracy (Figure 5a), the slopes of the learning curves were significantly greater for the attended location than for the unattended location for all attentional cue groups (exogenous: $p = 0.04$; endogenous/arrow: $p = 2.6 \times 10^{-7}$; endogenous/color: $p = 4.6 \times 10^{-5}$). The slopes for the attended location were also greater than for the divided-attended locations for the endogenous/arrow cue group ($p = 0.02$) and for the endogenous/color cue group ($p = 0.02$). Furthermore, the slopes of the learning curves for the divided-attended locations were greater than for the unattended location for all attentional cue groups (exogenous: $p = 0.025$; endogenous/arrow cue: $p = 2.1 \times 10^{-4}$; endogenous/color cue: $p = 0.02$).

Between-groups comparisons revealed that, for accuracy, the slopes for the attended location did not differ significantly among the three attentional cue groups ($p = 0.56$). On the other hand, the slopes for both the divided-attended and the unattended locations were greater for the exogenous cue group than for the endogenous/arrow ($p = 0.001$ and $p = 4.4 \times 10^{-4}$, respectively) and the endogenous/color ($p = 0.001$ and $p = 0.02$, respectively) cue groups. There was no significant difference in the slopes of the learning curves between the endogenous/arrow and the endogenous/color cue groups for either the divided-attended locations ($p = 0.936$) or the unattended location ($p = 0.18$).

For RT, in all attentional cue groups, the slopes of the learning curves at all locations were significantly different from zero (Table 2).

However, for the unattended location in the endogenous attention cue groups, comparable reductions in RT were also found on the incorrect trials (Supplementary Figure 1). This result, together with the absence of accuracy improvements, suggests that the improvements in RT at the unattended location in the endogenous attention cue

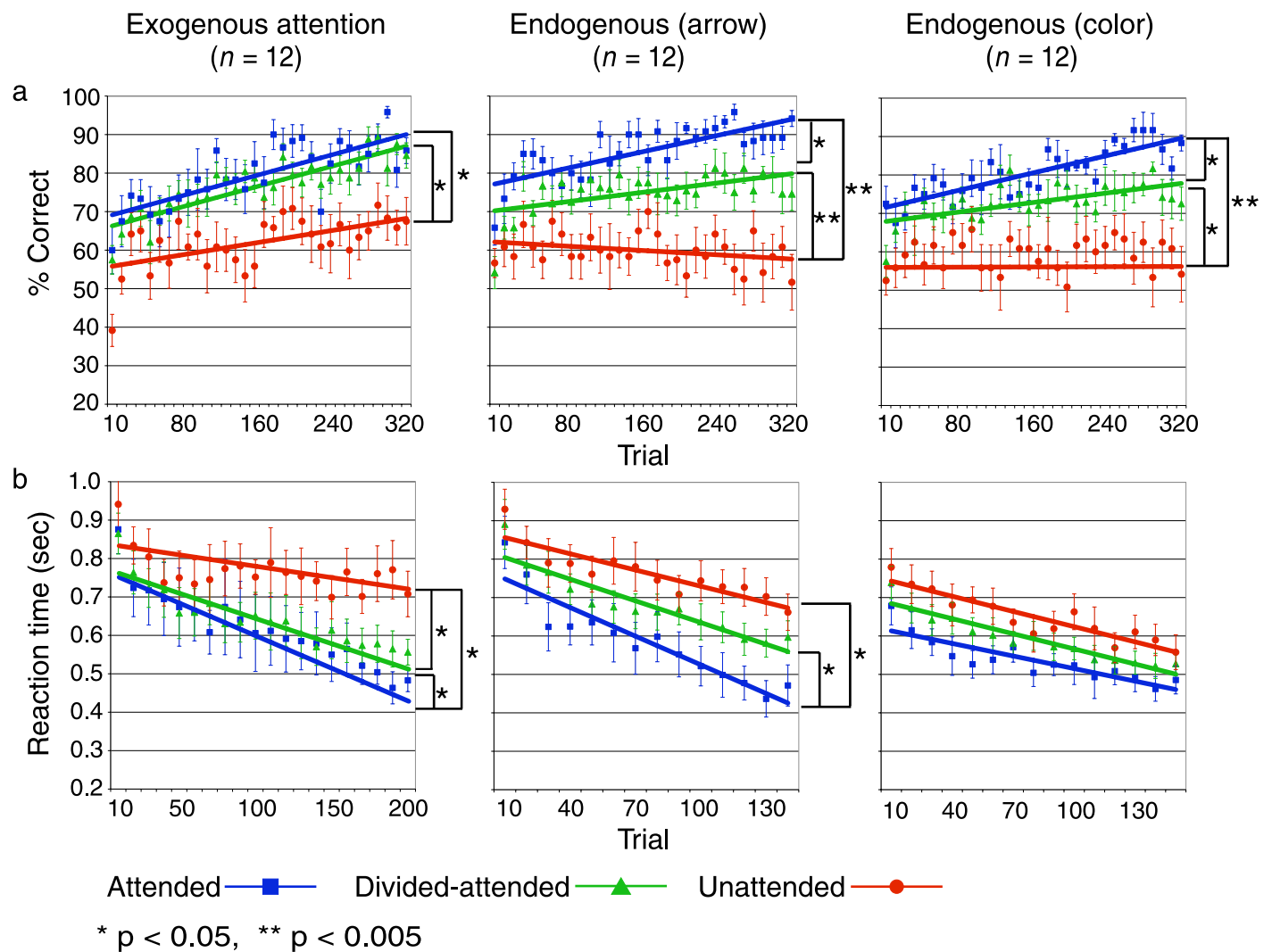


Figure 5. Behavioral changes during training. (a) Percent correct. (b) RT from correct trials. The p -values are the results of regression slope homogeneity tests between different levels of attention conditions within each attentional cue group. Error bars indicate *SEM*.

Level of attention	Type of attention		
	Exogenous	Endogenous (arrow cue)	Endogenous (color cue)
Attended	0.67* 7.2×10^{-11}	0.54* 2.2×10^{-12}	0.58* 1.7×10^{-10}
Divided-attended (combined)	0.67* 2.4×10^{-17}	0.31* 2.9×10^{-5}	0.32* 3.1×10^{-5}
Divided-attended (location 1)	0.63* 5.4×10^{-10}	0.33* 7.2×10^{-4}	0.33* 0.001
Divided-attended (location 2)	0.69* 1.7×10^{-11}	0.29* 0.004	0.31* 0.003
Unattended	0.40* 4.1×10^{-4}	-0.14 0.18	0.008 0.95

Table 1. Slope of learning curve: Percent correct increment per 10 trials (upper row). P -value for the test of null hypothesis: slope = 0 (lower row). Note: *, $p < 0.05$.

Level of attention	Type of attention		
	Exogenous	Endogenous (arrow cue)	Endogenous (color cue)
Attended	–0.017* 5.0×10^{-8}	–0.025* 2.44×10^{-10}	–0.011* 3.1×10^{-6}
Divided-attended (combined)	–0.013* 1.2×10^{-8}	–0.019* 1.7×10^{-10}	–0.013* 3.9×10^{-10}
Divided-attended (location 1)	–0.012* 1.0×10^{-7}	–0.018* 3.6×10^{-8}	–0.012* 2.0×10^{-5}
Divided-attended (location 2)	–0.014* 1.6×10^{-10}	–0.019* 3.4×10^{-9}	–0.013* 5.0×10^{-7}
Unattended	–0.006* 0.02	–0.014* 2.5×10^{-5}	–0.013* 2.5×10^{-7}

Table 2. Slope of learning curve: Reaction time reduction (s) per 10 trials (upper row). *P*-values for the test of null hypothesis: slope = 0 (lower row). Note: *, $p < 0.05$.

groups did not reflect improvements in performance of the task. Thus, as seen in the accuracy data, RT improved at attended and divided-attended locations for all subjects, irrespective of the attentional cue, but task-related improvement was found at the unattended location only for the exogenous attentional cue groups.

As shown in Figure 5b, comparisons of the slopes of the learning curves revealed that the differences between the attended and unattended locations in the exogenous ($p = 8.0 \times 10^{-6}$) and endogenous/arrow ($p = 0.005$) cue groups were significant. The differences between the attended and divided-attended locations in these two cue groups were also significant (exogenous: $p = 0.035$; endogenous/arrow: $p = 0.018$). Only for the exogenous attention condition, the slope for the divided-attended location was greater than for the unattended location ($p = 8.5 \times 10^{-6}$). There were no significant differences in the slopes of the RT learning curves among the levels of attention for the endogenous/color cue group.

Between-groups comparisons for the RT data revealed that the slope for the attended location was greater for the exogenous attentional cue group than for the endogenous/color cue group ($p = 1.5 \times 10^{-4}$). No significant differences in the slopes of learning curves were found for the attended location between exogenous and endogenous/arrow groups ($p = 0.131$) or between the endogenous/arrow and endogenous/color cue groups ($p = 0.401$). The slopes for neither the divided-attended nor the unattended locations differed significantly among the three attentional cue groups ($p = 0.305$ and $p = 0.08$, respectively).

Changes in contrast thresholds

The contrast thresholds measured before and after training for the two endogenous attention groups are shown in Figure 6a. A three (level of attention) \times two (pre- vs. post-training session) \times two (endogenous attentional cue: arrow vs. color) mixed-design ANOVA

showed that there were no significant main effects (attention level: $F[2,44] = 0.547$, $p = 0.582$; pre- vs. post-training session: $F[1,22] = 2.609$, $p = 0.121$; endogenous attentional cue: $F[1,22] = 0.333$, $p = 0.570$), and that there were no significant interaction effects either (level of attention \times endogenous cue: $F[2,44] = 0.569$, $p = 0.570$; pre- vs. post-training session \times endogenous cue: $F[1,22] = 0.937$, $p = 0.344$; level of attention \times pre- vs. post-training session: $F[2,44] = 0.454$, $p = 0.638$; level of attention \times pre- vs. post-training session \times endogenous cue: $F[2,22] = 0.264$, $p = 0.769$). Because two different endogenous attentional cues produced no significant differences, we combined the data from the two groups of subjects trained with the arrow and color cues in the comparison between exogenous and endogenous attention effects on improvements in contrast threshold after training. The contrast thresholds measured before and after training for the exogenous and endogenous (arrow cue and color cue groups combined) attention groups are shown in Figure 6b. A three-way (level of attention \times pre- vs. post-training session \times type of attention) mixed-design ANOVA revealed significant main effects of both level of attention ($F[2,68] = 4.399$, $p = 0.016$) and pre- vs. post-training session ($F[1,34] = 18.119$, $p = 1.5 \times 10^{-4}$). More importantly, the interaction effects of pre- vs. post-training session \times type of attention ($F[1,34] = 7.097$, $p = 0.012$) and level of attention \times pre- vs. post-training session ($F[2,68] = 4.633$, $p = 0.013$) were both significant. A two-way repeated measures ANOVA run on each type of attention group separately revealed that for the exogenous attention group there were significant main effects of level of attention ($p = 0.043$) and pre- vs. post-training session ($p = 0.011$) and also a significant interaction effect between the two factors ($p = 0.011$). For the endogenous attention group, neither significant main (level of attention: $p = 0.576$; pre- vs. post-training session: $p = 0.119$) nor significant interaction ($p = 0.628$) effects were found. The results of paired *t*-tests after the ANOVA confirmed that, for exogenous attention, there was significant improvement in contrast thresholds at the attended location ($p = 0.003$) and divided-attended

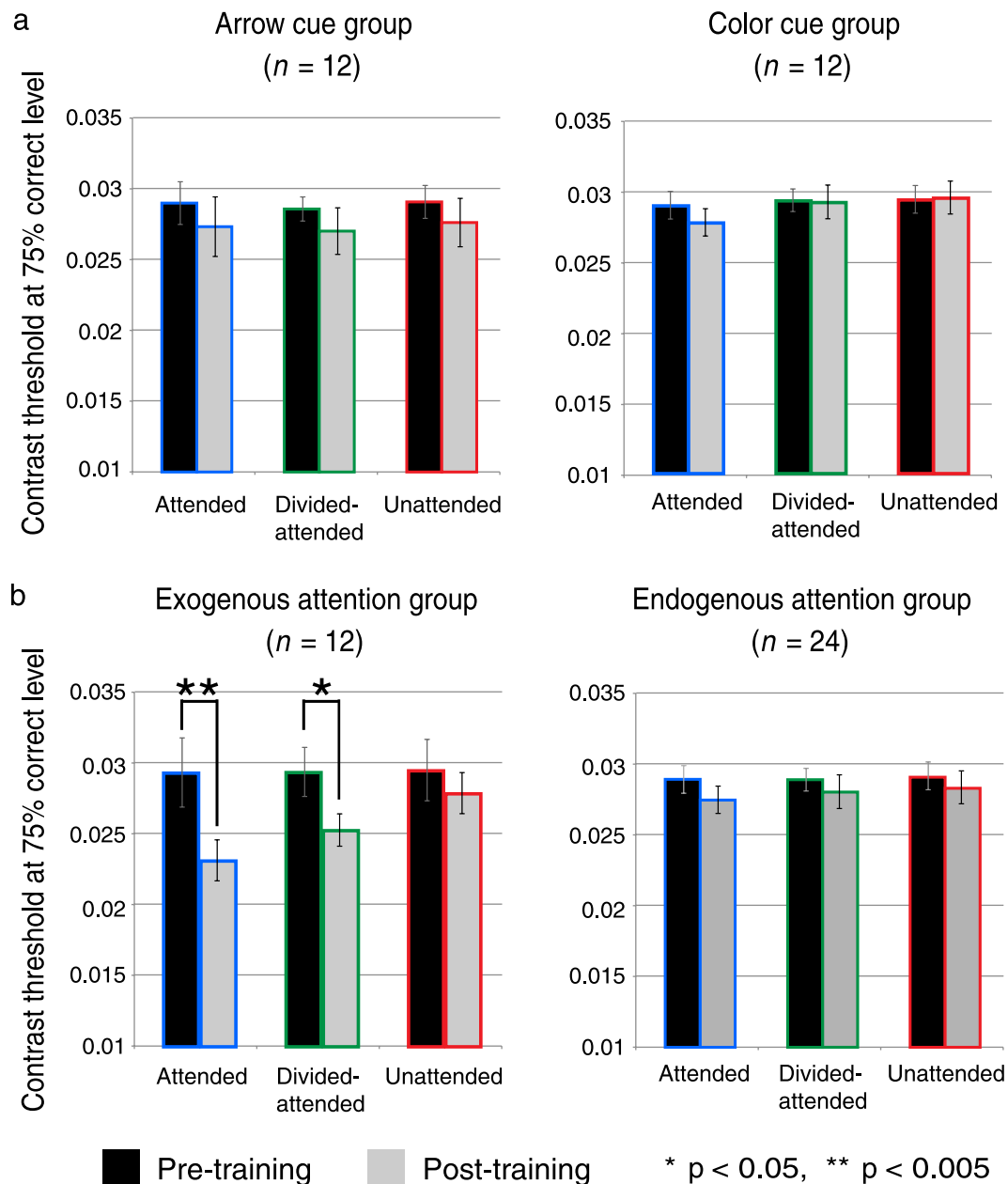


Figure 6. Changes in contrast thresholds measured pre- and post-training. Black-filled bars represent the pre-training contrast thresholds and gray-filled bars represent post-training contrast thresholds. (a) Endogenous/arrow and endogenous/color cue groups. (b) Exogenous and endogenous attention groups. The p -values are the results of paired t -tests. Error bars indicate SEM .

locations ($p = 0.015$) but not at the unattended location ($p = 0.316$). Furthermore, the improvement was greater at the attended location than at the divided-attended locations ($p = 0.046$). Thus, for the exogenous attention group, contrast thresholds improved at the attended and divided-attended locations after training but not at the unattended location. Moreover, the improvement at the attended location was greater than at the divided-attended locations. On the other hand, despite the perceptual learning seen during the training sessions for both attended and divided-attended conditions, as measured by accuracy, for the two groups of subjects trained with endogenous cues,

their contrast thresholds showed no improvement for either condition.

Correlation between behavioral changes during training and changes in contrast thresholds

As mentioned above, we found that for the endogenous attention groups accuracy improved during training, except at the unattended location where it did not. However, there was no significant improvement in

contrast thresholds for these groups at any locations. By contrast, significant improvements in the post-training contrast thresholds were found at the attended (mean = 0.0064) and divided-attended (mean = 0.0039) locations for the exogenous attentional cue group, as shown in Figure 6. For the estimates of contrast thresholds, within-subjects *SEM* ranged from 0.0012 to 0.0033 for the attended location and from 0.0011 to 0.0021 for the divided-attended location, which are considered quite small. Correlation analyses between detected changes in percent correct/RT during training and contrast thresholds measured before and after training for attended and divided-attended conditions in the exogenous attention group revealed that there was no significant correlation for either attended (percent correct vs. threshold: $r = 0.29$, $p = 0.35$; RT vs. threshold: $r = 0.14$, $p = 0.66$) or divided-attended (percent correct vs. threshold: $r = 0.37$, $p = 0.23$; RT vs. threshold: $r = 0.04$, $p = 0.91$) conditions, although improvements for this group were seen in both behavior during training and post-training contrast thresholds. Thus, the behavioral changes observed during training cannot be explained by improvements in subjects' contrast sensitivity at the stimulus locations measured by the current method.

Eye position during the experiment

As shown in Table 3, the subjects' averaged gaze durations at the stimulus locations were less than 0.1%, while the gaze durations at central fixation were ~90% for both types of attention conditions.

The results indicate that subjects maintained their fixation on the central fixation spot, as instructed. A four (area of interest) \times two (type of attention) mixed-design ANOVA revealed a significant main effect of area of interest ($F[1, 32.010] = 4637.024$, $p = 1.0 \times 10^{-103}$); however, there was no significant main effect of type of attention ($F[1, 32] = 1.154$, $p = 0.291$) nor a significant

interaction between area of interest and type of attention ($F[1, 32.010] = 1.238$, $p = 0.274$). The result indicates that there was no difference in the pattern of gaze between exogenous and endogenous attention groups. Paired *t*-tests following the ANOVA confirmed that gaze duration was significantly longer at the central fixation area than at any of the stimulus locations ($p < 1.0 \times 10^{-37}$). The gaze durations at the four stimulus locations were not significantly different from each other ($p > 0.1$). Thus, the difference in behavioral improvement among the three different levels of attention (attended, divided-attended, unattended) cannot be attributed to different amounts of gaze time at the different locations. The difference in contrast threshold improvement between the subjects trained with exogenous and endogenous attentional cues also cannot be due to differences in gaze times.

Discussion

The goal of the current study was to assess the effects of exogenous and endogenous attention on perceptual learning of an orientation discrimination. We found that both exogenous and endogenous attention facilitated perceptual learning, as reflected by enhanced accuracy over the course of training for the attended and divided-attended conditions compared to the unattended condition. Moreover, the rates of perceptual learning for the attended condition during training were comparable for both types of attention. A reduction in RT was also greater for the attended than for the unattended condition, except for the endogenous/color attentional cue group. Furthermore, the magnitude of improvement in accuracy, as indicated by the slopes of learning curves for the endogenous cue groups, differed between the attended and divided attended conditions, which is consistent with the finding that perceptual performance under divided-attended conditions is lower than under attended conditions. For example, Lu and Doshier (1998) demonstrated lower contrast thresholds for attended stimuli than for divided-attended stimuli. In the current study, we also confirmed that, early in training, the accuracy level was higher and RT was shorter at attended locations than at divided-attended locations. Thus, the current study demonstrated that not only perceptual performance per se but also the improvements during perceptual learning can be a function of the level of attention.

Although accuracy and RT improvements were also found for stimuli at the unattended location in the exogenous attention condition, this may have been caused by a lack of experimental control of attention in our study. Because all the training stimuli were equally task-related in the paradigm with exogenous attentional cues, it is possible that subjects intentionally divided their attention to all the stimulus locations. The comments from all the

Areas of interest	Type of attention	
	Exogenous	Endogenous
Percent fixation ^a	92.01	89.00
Percent attended ^b	0.02	0.08
Percent divided-attended ^c	0.02	0.07
Percent unattended ^d	0.02	0.04
Percent other ^e	7.93	10.81

Table 3. Averaged duration of gaze time for each area of interest (duration = gaze time / total experiment time). Note: ^aThe area was defined by a 3×3 degree square around the fixation circle in the middle of the screen. ^b, ^c, ^dThe stimulus locations. ^eThe area outside of the four areas of interest, (a)–(d).

subjects in the exogenous attention cue group support this view, i.e., they tried to spread their attention among all the training stimuli. On the contrary, the subjects in the endogenous attention cue groups reported that they followed the instruction and attended the cued locations.

In our previous study (Mukai et al., 2007), we found that subjects who subsequently learned had initially higher levels of activation in dorsal frontoparietal areas related to endogenous attention (Corbetta & Shulman, 2002) than subjects who did not learn. We speculated that the subjects who learned relative to those who did not deployed endogenous attention to the stimulus and task at hand during the initial period of training, and that this led to their successful perceptual learning. Because visual information processing has a limited capacity, attention acts to bias competition among all the visual inputs in favor of the attended stimulus (Desimone & Duncan, 1995). The results of the current study extend that finding by demonstrating that a stimulus with such an attentional bias is not only processed preferentially and thus perceived more accurately than an unattended stimulus but also results in increased accuracy after repetitive experience relative to an unattended stimulus.

The importance of attention is also evident for novel skill execution and learning (Cohen, Ivry, & Keele, 1990; Fisk & Schneider, 1984; Nissen & Bullemer, 1987; Schneider & Shiffrin, 1977; Shiffrin, Dumais, & Schneider, 1981; Shiffrin & Schneider, 1977). Schneider et al. have argued that during motor skill acquisition, behavioral performance is based on an attentionally controlled processing system but that well-learned performance is based on an automatic processing system that does not require attentional guidance of behavior. Their recent human imaging study (Hill & Schneider, 2006) showed a reduction of activation in posterior parietal brain areas related to attentional control, as a function of a motor skill acquisition. The result is comparable to what we found previously for perceptual learning (Mukai et al., 2007), that is, a negative correlation between the level of activation in frontoparietal attention-related areas and the degree of perceptual learning. Because perceptual learning and motor-skill learning are both implicit, procedural tasks, the mechanisms subserving the two may work in a similar manner, such that attention may facilitate the successful acquisition of both.

Although we have shown the importance of attention in perceptual learning, data from Watanabe et al. seem at odds with this conclusion. They reported that behavioral improvements can be achieved for task-irrelevant (i.e., unattended) visual motion stimuli presented at a subthreshold level (Nishina et al., 2007; Seitz, Kim, & Watanabe, 2009; Seitz & Watanabe, 2003; Watanabe et al., 2002, 2001). Why did perceptual learning occur for an unattended stimulus in their studies but not in our current study using endogenous attentional cues? Tsushima, Seitz, and Watanabe (2008) have proposed an answer to the question:

while signals of an attended stimulus are enhanced, signals of an unattended stimulus would normally be suppressed. However, if signals of an unattended stimulus are at a subthreshold level, then the signals would be too weak to be suppressed. Hence, without attentional suppression, the signals of an unattended stimulus can be strong enough to be processed, and perceptual learning would occur for that unattended stimulus after repeated exposures with it. In the current study, the contrast of the stimuli was at the level of ~75% accuracy for our orientation discrimination task. Thus, signals from the stimulus at the unattended location should have been suppressed and consequently too weak to induce perceptual learning (Paffen, Verstraten, & Vidnyanszky, 2008). According to this logic, the results of the two sets of studies, although seemingly at odds, are in fact compatible.

In the current study, we also demonstrated a dissociation in the effects of exogenous and endogenous attention. Only exogenous attention deployed during training resulted in improved contrast thresholds measured in post-training compared to pre-training. In previous studies, mixed results have been reported regarding improvements in contrast discrimination thresholds during perceptual learning (Adini, Sagi, & Tsodyks, 2002; Dorais & Sagi, 1997; Sagi, Adini, Tsodyks, & Wilkonsky, 2003; Yu, Klein, & Levi, 2004). The exact conditions under which such improvements occur are still unclear. The improvement in contrast thresholds we observed was greater at the attended location than at the divided-attended locations. However, across subjects in the exogenous attention group, these improvements in contrast thresholds did not significantly correlate with the improvements in accuracy/RT during training. In addition, the learning rates in accuracy at the attended location for the endogenous attention groups were comparable with that for the exogenous attention group, whereas no significant improvements in contrast thresholds were found for the endogenous attention groups.

However, it is possible that we failed to detect endogenous attention-related improvements in contrast threshold due to the method we employed. That is, there was only one Gabor patch presented during contrast threshold measurements, whereas four Gabor patches were presented simultaneously during training. If endogenous attention affects perceptual learning predominantly through distractor-suppression mechanisms, then presenting only one Gabor patch during contrast measurements may have made our procedure insensitive to detect the effects of endogenous attention.

Given the methods we employed, we found significant improvements in contrast threshold at the attended and divided-attended locations only in the exogenous attentional cue group. Furthermore, we found no significant correlation between performance improvements during training and contrast-threshold improvements at the attended and divided-attended locations in the exogenous

attentional cue group. Therefore, the contrast threshold improvements found for the attended condition in the exogenous attention group cannot be explained by the rates of learning in accuracy during training. Collectively, the results suggest that perceptual learning as measured by threshold improvements is qualitatively different from perceptual learning as measured by accuracy and RT during training. Exogenous attention, but not endogenous attention, appears to play a key role in the former. This view implies that these two measures of perceptual learning depend on different neural mechanisms. Support for this view comes from the study by Ling and Carrasco (2006). They used a similar attentional cueing paradigm as the current study and showed differential effects of exogenous and endogenous attention on contrast response functions. According to their results, exogenous attention operates via both contrast- and response-gain mechanisms, whereas endogenous attention operates via a contrast-gain mechanism only (however, it is still controversial whether contrast gain or response gain, or a combination of both mediate attentional effects on the contrast response function; see also Huang & Dobkins, 2005; Morrone, Denti, & Spinelli, 2004; Pestilli, Ling, & Carrasco, 2009; Reynolds, Pasternak, & Desimone, 2000; Williford & Maunsell, 2006). The view that exogenous and endogenous attention facilitate perceptual learning via different neural mechanisms is also in line with the findings of Corbetta and Shulman (2002). Based on human brain imaging data, they have proposed two segregated neural systems for attention: a dorsal posterior parietal and frontal network for endogenous attention and a temporoparietal and ventral frontal network, mainly in the right hemisphere, for exogenous attention. If the signals of exogenous and endogenous attention are mediated by different networks, this might be reflected in dissociable effects on perceptual learning.

Conclusion

The current study has demonstrated that both exogenous and endogenous attention facilitate behavioral improvements on an orientation discrimination task, as measured by accuracy and reaction time, but only exogenous attention increases sensitivity, as measured by contrast threshold, to the trained stimulus. In addition, there was no significant correlation between the behavioral improvements during training and enhancements of contrast sensitivity obtained post-training. We propose that both exogenous and endogenous attention play an important role in perceptual learning in terms of enhancing the procedural aspects of the task, but that enhanced sensitivity to the target stimulus is affected by exogenous

attention only. Future studies should elucidate the neural underpinnings of exogenous and endogenous attention in perceptual learning.

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