Perception, 2014, volume 43, pages 549–568

doi:10.1068/p7660

Effects of attention on visible and invisible adapters

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Received 30 November 2013, in revised form 19 May 2014

Abstract. It has been shown that attention can modulate the processing of a stimulus, even when it is invisible (Bahrami, Carmel, Walsh, Rees, & Lavie, 2008, *Perception*, **37**, 1520–1528). Previous studies, however, investigated the effect of spatial attention on the processing of only invisible items. Thus, it remains unclear how the effect of spatial attention is distributed over visible and invisible items when these items are simultaneously attended at the same location. In the present study we addressed this question using two types of adapters, one visible and one invisible, and compared how attention affected the processing of each adapter. Moving gratings and tilted gratings were presented to each eye; the moving ones were dominant over the tilted ones. Both types of stimuli were located on the left and right sides of a fixation cross, and the participants performed a task that modulated their attention to one side or the other. In experiment 1 they were asked to detect the contrast decrement of one of the moving gratings, and in experiment 2 they detected a dot that was presented to both eyes. We found that attention increased the amount of motion aftereffects induced by the visible adapters. However, we did not find effects of attention on tilt aftereffects from the invisible adapters. Finally, in experiment 3 we found that attention successfully increased the amount of tilt aftereffects when the adapters were not suppressed. These findings suggest that spatial attention is more likely to influence visible items than invisible items in the same location. We also found that invisible items do not interfere with the attentional modulation of the processing of visible items.

Keywords: spatial attention, MAE, TAE, visibility

1 Introduction

The phenomena of visual attention and visual consciousness have been thought of as tightly entwined. According to Posner (1994), attention is the gatekeeper of our conscious experience. When we attend to visual stimuli, the quality of our experience concerning them can change; attention can increase the apparent contrast of stimuli (Ling & Carrasco, 2006) or combine visual features to produce a complete mental picture, in a process known as feature binding (Treisman & Gelade, 1980). However, visual attention can impair our visual experience when it is not properly allocated. We fail to detect a subtle change in a visual scene when we do not attend to the locus of change (Simons & Levin, 1997) or cannot identify a target presented immediately after an attended probe (Raymond, Shapiro, & Arnell, 1992). Moreover, patients who have damage to an attention-related brain area show a loss of conscious experience of a sensory event occurring in the contralateral side of their damaged brain (Driver & Vuilleumier, 2001).

Recent studies, however, have suggested that attention and conscious experience are dissociated. Attention can influence invisible stimuli as it does visible stimuli (Kentridge, Nijboer, & Heywood, 2008; Montaser-Kouhsari & Rajimehr, 2005; Tapia, Breitmeyer, Jacob, & Broyles, 2013). Attending to invisible stimuli can increase the amount of adaptation to their properties, such as orientation (Bahrami, Carmel, Walsh, Rees, & Lavie, 2008; Montaser-Kouhsari & Rajimehr, 2005) or gender (Shin, Stolte, & Chong, 2009). It was also found that both spatial and featural attention can affect the processing of a masked probe, despite the fact

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that it is not visible (Tapia, Breitmeyer, & Shooner, 2010; Tapia et al., 2013). Furthermore, Watanabe et al. (2011) found that fMRI responses to unconscious information were more activated when the stimuli were attended compared with when they were not. These findings suggest that attention does not necessarily serve as a gatekeeper of our conscious experience.

Among the various ways to make stimuli invisible, several researchers have employed interocular suppression, induced by presenting two dissimilar images to each eye. When interocular suppression occurs, one image is consciously perceived while the other is suppressed (Helmholtz, 1910; Levelt, 1967; Sengpiel, Freeman, & Blakemore, 1995). Drawing on this intriguing phenomenon, several studies found that the effect of attention can permeate to suppressed images, which are presented without conscious perception. For example, Kanai, Tsuchiya, and Verstraten (2006) showed that featural attention can facilitate the processing of invisible stimuli. In their study the degree of tilt aftereffect (TAE) was higher when invisible adapters had the same orientation compared with when the orientation was different. Spatial attention can also influence the processing of invisible stimuli. When spatial attention is directed to where an invisible adapter is presented, the aftereffect from the invisible adapter increases compared with when attention is directed to another location (Shin et al., 2009).

Although previous studies have shown that attention can be allocated to visual stimuli processed under interocular suppression (Bahrami et al., 2008; Kanai et al., 2006; Shin et al., 2009), it remains unclear how the effect of attention is distributed over two competing items. According to previous studies, it is likely that the dominant items benefit more from an attentional boost than do the suppressed items. Ling and Blake (2012) suggested that both attention and rivalry are governed by the common mechanism of normalization. According to this normalization model, a dominant stimulus acts as a modulatory attentional field, withdrawing attentional influence on the suppressed item. The degree of attentional influence depends on the size of the attentional field. Applied to the present study, this model predicts that there should be a response gain shift to the suppressed item, as the attentional modulatory field (the dominant item) is as small as the suppressed item. Furthermore, the reverse hierarchy hypothesis suggests that attention has a greater effect at higher stages of visual processing as compared with early stages (Hochstein & Ahissar, 2002). Because the dominant item is more likely to reach a higher stage of visual processing with the suppression of the competing image (Sakuraba, Sakai, Yamanaka, Yokosawa, & Hirayama, 2012), attention influences the processing of dominant stimuli more than it does suppressed stimuli. Given the marked reduction of the gain for suppressed stimuli and the stronger attentional influence on dominant stimuli, the effect of attention will be much stronger for dominant stimuli than for suppressed stimuli.

In the present study we investigated whether there is a difference in the degree to which the processing of visible and invisible stimuli is affected by spatial attention. We used two types of adapters, dominant and suppressed under binocular rivalry, to induce a motion aftereffect (MAE) and a TAE, respectively. To compare the effects of attention between the dominant and suppressed adapters, these adapters were presented in the corresponding location and attended simultaneously. To manipulate spatial attention, observers were instructed to detect a contrast decrement on one of two dominant adapters (experiment 1), and a dot appeared in the visual field of both eyes (experiment 2). We then measured the amounts of MAE and TAE from the attended and unattended locations. Finally, we measured the effect of attention on TAE without the MAE adapters so that the tilted adapters were visible (experiment 3). To preview our findings, in both experiments 1 and 2 we found that attention had a stronger effect on the processing of the MAE adapters than on that of the TAE adapters. Nevertheless, in experiment 3 attention increased the amount of TAE when the TAE adapters were visible. Therefore, spatial attention primarily influences adaptation from dominant items.

2 Experiment 1

In experiment 1 we investigated how the effect of attention is allocated to visible and invisible adapters under interocular suppression. We chose to employ moving gratings as the visible adapters and tilted gratings as the invisible adapters for the following reasons. First, it is known that both types of aftereffects, MAE and TAE, are modulated by attention (for MAE, Nishida & Ashida, 2000, and for TAE, Spivey & Spirn, 2000). Therefore, we expected that the aftereffects from both adapters in the attended location would be enhanced. Also, for one image to be suppressed by the other, there should be differences in the strength levels of the stimuli between the two adapters. Using moving and tilted adapters satisfies this constraint because a motion signal is stronger than a static signal. Finally, it is necessary to ensure that the aftereffects from the suppressed adapters can survive through interocular suppression, and it was shown that TAE can be measured even when an adapter is suppressed (Wade & Wenderoth, 1978).

To manipulate spatial attention, we used a contrast-decrement detection task (CDD task) on the dominant adapter (Shin et al., 2009). The visible and invisible adapters were located on the left and right sides of a central fixation cross, and participants performed the task on either the left or right side of the fixation cross. While the moving gratings drifted at full contrast, the contrast decreased briefly and the participants were instructed to detect this change. To equate the difficulty of the task, we measured the threshold of the contrast decrement and adjusted the amount of contrast decrement for each participant in the main experiment. After adaptation to the visible and invisible adapters, the amounts of MAE and TAE were measured in both the attended and unattended locations. The difference in the amount of aftereffects between the two locations was defined as the effect of attention.

2.1 *Methods*

2.1.1 *Participants.* Twelve Yonsei University students, including the first author, participated in this experiment; all except the author received a monetary reward for their participation. All had normal or corrected-to-normal vision. All except the author were naive to the purposes of the study and gave written informed consent after receiving an explanation of the procedures. Every aspect of this study was approved by the Institutional Review Board of Yonsei University.

2.1.2 *Apparatus.* All of the stimuli were created using the Psychophysics Toolbox of MATLAB (Brainard, 1997; Pelli, 1997) and were presented on two Samsung 22″ CRT monitors with a refresh rate of 85 Hz. A conventional mirror stereoscope was used to present different stimuli to each eye separately. The luminance profile of the monitors was gamma-corrected and linearized. Participants' heads were fixed on a chin-and-forehead rest at a distance of 60 cm from the monitors. At this distance, one pixel was subtended at approximately 0.025 deg.

2.1.3 *Stimuli.* Circular sinusoidal gratings were used to induce MAE and TAE. The radius of the grating was 1 deg, and the distance from the center of the grating to the fixation cross was 2.5 deg. Gratings were always surrounded by a checkerboard frame whose width was 0.15 deg, and the contrast of the frame was 48.32% (all of the contrast information reported here was calculated using the Michelson formula, except the contrast of the dots for the detection tasks in experiments 2 and 3). The motion adapters had a spatial frequency of 6 cycles deg^{-1} and a contrast of 99.28%. They drifted at a speed of 1 deg s^{-1} either leftward or rightward (figure 1a). For the tilted adapters, we used two sine-wave gratings that were tilted 15° either clockwise or counterclockwise. The spatial frequency of the gratings was 3 cycles deg^{-1}, and their contrast was either 5.68% or 8.1% depending on each participant's contrast sensitivity (figure 1a).

To measure the amount of MAE, we used a counterphase grating. It was a linear sum of the two gratings that had the same spatial and temporal frequency but drifted in opposite directions (figure 1b). The MAE seen in a counterphase grating could be nulled by increasing the contrast of one component that drifted in a direction opposite to the MAE direction. The contrast of each component was changed during every trial by 4%, but the sum of the contrast of each remained the same, at 29.10%. The gratings used to measure TAE had the same features as those that evoked TAE, except that their orientation varied by ±2~3° (figure 1c).

We took several measures to render the motion adapters predominantly visible when the two types of adapters appeared in the same location via different eyes. First, motion adapters were presented to the dominant eye of each participant. Second, compared with tilted gratings, whose contrast was 5.68% or 8.1%, motion gratings had a contrast of 99.28%. Third, the gratings appeared 15 s after the moving gratings were presented. In addition, the contrast of tilted gratings was ramped up gradually from 0% to full contrast so as not to change the visibility of the motion gratings. To verify that these measures rendered the tilted gratings effectively invisible, we conducted a visibility test after the main experiment.

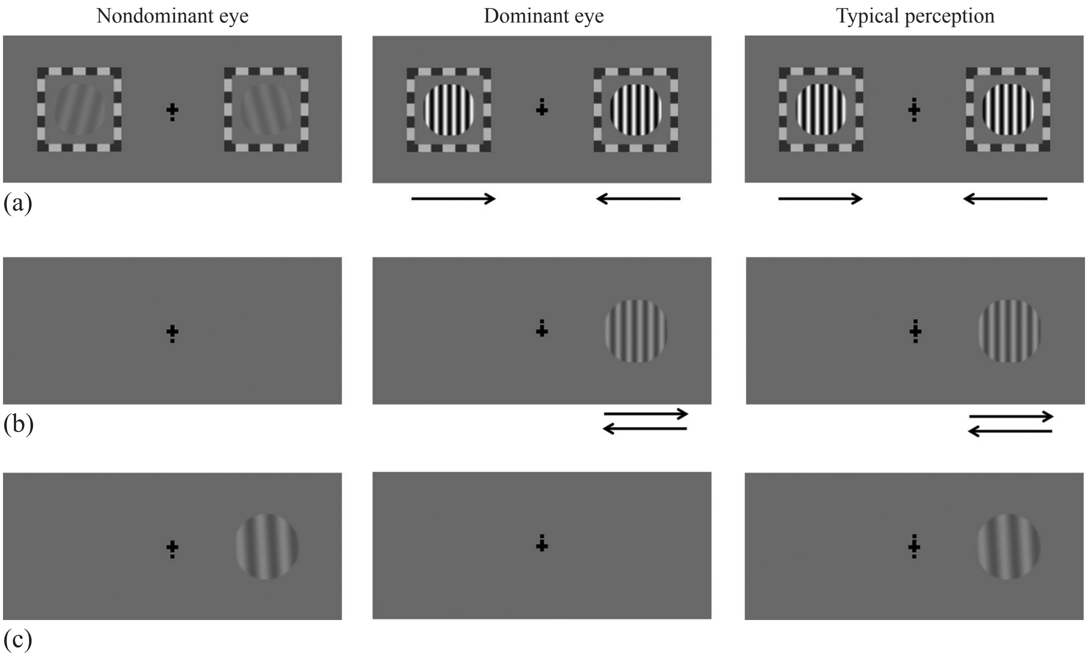


Figure 1. The stimuli used as the adapters and the testers in measuring the motion aftereffect (MAE) and the tilt aftereffect (TAE) (the left and middle columns) results and the typical percept for them (the right column). Arrows indicate the direction of motion. (a) The tilted adapters presented to the nondominant eye and the moving adapters presented to the dominant eye. (b) The test stimuli used to measure the amount of MAE. There was no stimulus except for the fixation cross in the nondominant eye when the MAE tester was presented to the dominant eye. (c) The test stimuli used to measure the amount of TAE.

2.1.4 *Procedure.* There were three sessions in this experiment: (1) the measurement of the CDD threshold, (2) the measurement of MAE and TAE, and (3) the measurement of the visibility of the suppressed adapters. Before each session, there was a 6 min period of dark adaptation. In this period only a fixation cross was presented. Before the experiment, we tested eye dominance for each participant using a variation of the Miles test (Miles, 1930; Roth, Lora, & Heilman, 2002).

2.1.4.1 *Measurement of the CDD threshold.* We measured the CDD threshold of each participant to equate the difficulty level of the detection task in the main experiment across all participants. This session started with a flicker of the checkerboard frame for 500 ms in a to-be-attended location, which indicated where participants had to attend and perform a detection task. After the checkerboard flickered as a location cue, two gratings that drifted either leftward or rightward were presented on either side of the fixation cross for 5 s. During those 5 s, the contrast of the attended grating decreased for 110 ms at a random point between 500 ms and 3500 ms after the onset of the motion grating task. Participants were asked to press the number key '5' as soon as they detected the decrement. We used two interleaved staircases with a two-up and one-down procedure to measure the amount of decrement in the contrast to reach an accuracy rate of 71% (Levitt, 1971). Whenever participants were correct, we decreased the amount of decrement in the contrast by 4%, whereas it was increased by 4% whenever they were incorrect. Each staircase was terminated when there were 17 reversals. If participants failed to detect the decrement of the contrast, a beep was sounded as feedback. We measured CDD thresholds on both the left and right sides of the fixation cross and averaged the last four reversals of each staircase from both sides to determine the CDD threshold for each participant.

2.1.4.2 *Measurement of MAE and TAE.* In the main experiment we measured MAE and TAE in separate blocks. There were two TAE blocks (the invisible adapter condition) depending on the location the participants attended, ie left or right. MAE was measured in four different blocks (the visible adapter condition), which were counterbalanced depending on the location to attend (left or right) and the presence of the suppressed adapters (with or without the suppressed adapters). The order of the blocks was randomized for each participant. Participants performed one or two blocks a day, and there was a break of 6 min between the blocks to minimize the influence of the previous adaptation. Each block consisted of adaptation and test phases, and there was no break between the two phases (figure 2a).

Each block started with dark adaptation, lasting 6 min. After this dark adaptation phase, a fixation cross was presented in the center of the screen and participants were instructed to press the space bar to initiate a trial. When they started, two checkerboard frames were presented on either side of the fixation cross. One flickered for 500 ms as a cue for the task location. After the flicker, two gratings were presented inside of each checkerboard frame to the dominant eye so that two motion adapters appeared. The gratings drifted either leftward or rightward so that participants were adapted to the opposite direction of motion in each location. Participants were instructed to attend to the location where the frame had flickered and perform a CDD task on the motion adapter presented in the cued location. After 15 s, two tilted gratings were presented to the suppressed eye in the same location where the motion adapters were presented (only in the suppressed adapter-present condition). The contrast of the tilted gratings was gradually increased for 5 s, remaining at 5.68% or 8.1% for 10 s. Note that we set the default contrast of the tilted gratings at 5.68%, but increased it about 1.5-fold if the participants could not detect the tilted gratings in the test phase. If the orientation of the tilted grating presented to the left of the fixation cross was tilted clockwise, the right one was tilted counterclockwise, and vice versa. The adaptation phase lasted 90 s, with the 30 s of the above procedure repeated three times without a break (figure 3a). During the adaptation period of 90 s, contrast decrements randomly occurred 27 times.

After the adaptation phase, the test phase followed without a break. We measured MAE or TAE depending on the visibility condition of the adapters. For both cases we used two interleaved staircases for each location and tested both the attended and unattended locations in a random order. In other words, four staircases were carried out within a block: two interleaved staircases for the attended location and the other two for the unattended location (figure 2b). Following each test trial, a top-up adaptation of 10 s ensued. The top-up adaptation

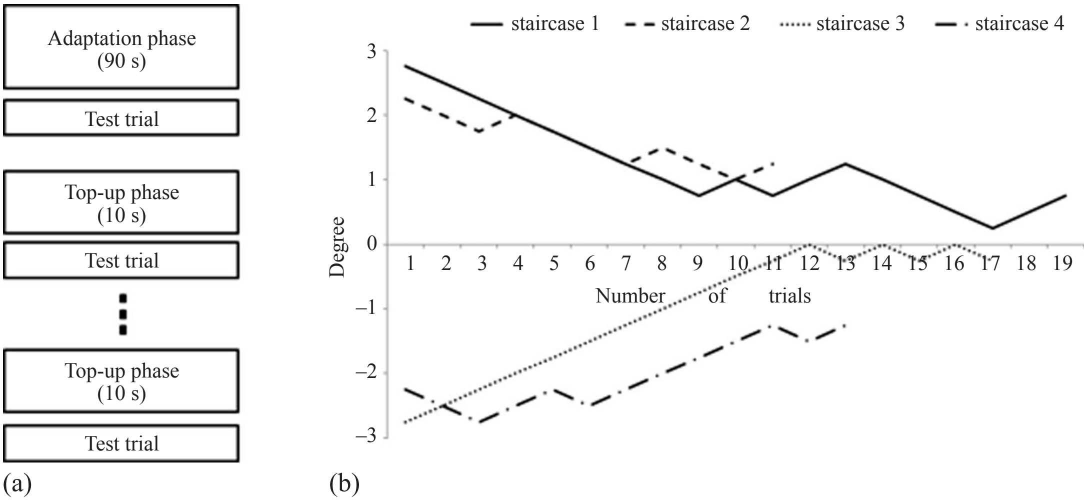


Figure 2. (a) The procedure of the blocks to measure the aftereffects. The initial adaptation phase lasted 90 s, followed by the first test trial. Next, each ensuing test trial was preceded by a top-up phase (10 s), which was repeated until all four staircases had six reversals (b).

was similar to the adaptation phase except that the tilted gratings gradually appeared for 5 s from the beginning of the phase and remained for 5 s. Contrast decrements occurred three times during the 10 s of the top-up phase. Specific descriptions of each type of block are given below.

Figure 3b illustrates how the test trial was processed. After either an adaptation (for the first trial) or a top-up adaptation period, the checkerboard frame of one location disappeared to indicate the location where the test stimulus would be presented. After 200 ms, the test stimulus was presented at the location that was cued by the disappearance of the checkerboard frame. The frame of the opposite location also disappeared. The test grating with two opposite directions (leftward and rightward) was presented for 1 s randomly in either the attended or unattended location. Participants were instructed to report the direction of motion (either leftward or rightward) that came to mind first. Four staircases, two for the attended location and the others for the unattended location, ran in a block, and one of them was randomly chosen for each trial. The blocks of each condition were performed until all of the staircases reached six reversals with the one-up and one-down procedure (figure 2b). The contrasts of both the MAE direction and the opposite direction components were averaged from the last four reversals. We defined the strength of MAE by dividing the contrast of the MAE-direction component by that of the other component.

For the blocks used to measure TAE, we used a tilted grating, which was presented briefly (200 ms) in either the attended or unattended location. As in the MAE blocks, the checkerboard frame indicated where the test stimulus would be presented by disappearing in advance. Participants reported whether the test grating was tilted clockwise or counter-clockwise by pressing the number keys ‘4’ and ‘6’, respectively. As in the blocks used with the MAE measurement, four independent staircases (two for each location) were executed until all of them reached six reversals. The step size for each staircase was 0.25°, indicating that the orientation of the test gratings was shifted in the opposite direction of the participants’ report by 0.25°. The amount of TAE was defined as the average orientation of the last four reversals.

To control for individual differences in orientation discrimination, we measured the orientation bias of each participant. Without any adaptation, we presented the test stimulus in the same way as the TAE blocks. We used four staircases with a step size of 0.25°,

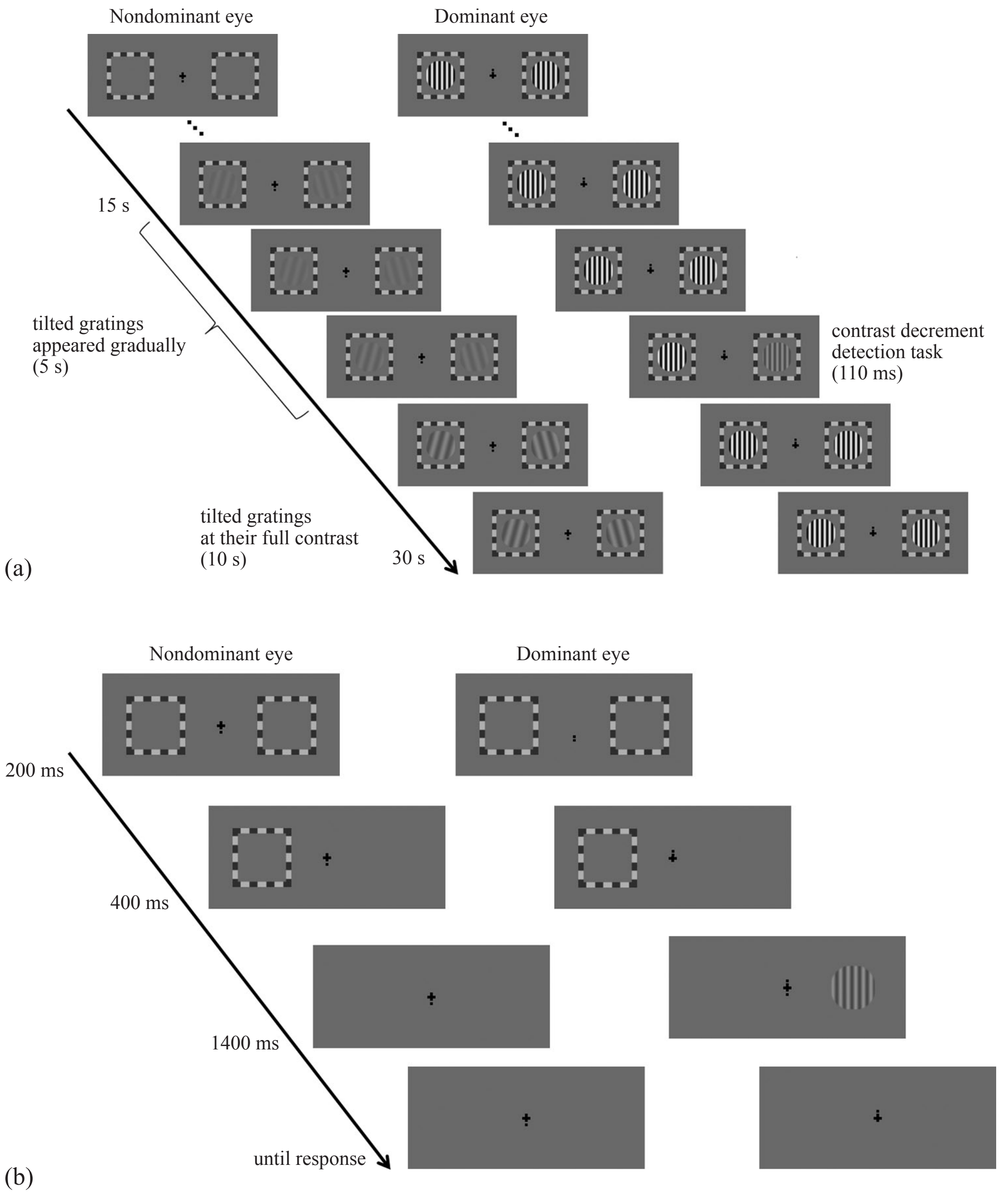


Figure 3. The procedure of the main blocks to measure the aftereffects in experiment 1: (a) the 30 s illustration of the initial adaptation, which was repeated three times in the initial adaptation phase. The moving adapters presented to the dominant eye drifted either leftward or rightward. For the adapter of the cued location, its contrast was randomly decreased, and participants were instructed to detect it whenever it occurred (27 times for the entire adaptation phase). For the other eye, the tilted adapters started to appear gradually 15 s after the onset of the moving gratings. After 5 s, they reached their full contrast and lasted for 10 s. (b) An example of a test trial to measure motion aftereffect (MAE). After the adapters disappeared, leaving only the checkerboard frames (200 ms), one of the checkerboard frames disappeared to indicate the location where the test stimulus would be presented. After 200 ms, the test stimuli, which had both the MAE direction and the opposite direction of drifting, appeared for 1 s. Upon the onset of the test stimulus, the checkerboard frame of the other location also disappeared. After the presentation of the test stimulus, the screen with the fixation cross lasted until the participant gave a response.

with two of them executed for each location—that is, the left and right sides of the fixation cross. Participants reported the orientation of the test grating as they did in the blocks of the TAE measurement. The orientations of the last four reversals were averaged, with the result defined as the point of subjective equality (PSE).

2.1.4.3 *Measurement of the visibility of the tilted gratings.* After the main experiment, we tested the visibility of tilted gratings. Here, the adaptation phase of the main experiment was presented without a CDD task. Participants were instructed to pay attention to their percept and keep the number key '5' depressed while they perceived a tilted grating. The visibility of the tilted grating was calculated as the time during which the participants pressed the key divided by the time during which the tilted gratings were presented.

2.2 *Results and discussion*

We examined the effect of attention on the amount of adaptation from visible and invisible adapters, which were measured on drifting and tilted gratings, respectively. Before analyzing the aftereffects of the two types of stimuli, we checked participants' performance levels on a CDD task to ensure that they actually attended to the instructed location. In addition, the visibility of the tilted gratings was analyzed to confirm that our modulation of visibility via interocular suppression was successful.

Participants' CDD thresholds to achieve 71% accuracy on the CDD task varied from 19.62% to 62.92%. We used the thresholds of each participant as the amount by which to decrease the contrast of the drifting gratings for the CDD task in the main experiment. With the thresholds of the contrast decrement, we aimed to adjust the difficulty of the CDD task so that it was equivalent across participants. Despite our efforts, there were considerable individual differences during the performance of the CDD task; the highest detectability was 59.18%, and the lowest was 21.76% (on average, the result was 40.6% with a standard deviation of 12%). We suspect that significant adaptation during the main experiment made the task more difficult in the main experiment. We also checked whether the degree of attentional engagement was similar across TAE and MAE blocks by examining the performances on the CDD task. The performance levels under the two conditions did not differ significantly ($t_{11} = -1.75$, $p = 0.864$).

The results of the visibility check experiment showed that the tilted gratings were rendered invisible via interocular suppression; on average, they were visible for 10.6% of their presentation duration with a standard deviation of 12.69%. The degree of visibility was different across participants; the proportion of perceiving the tilted gratings ranged from 0% to 43%. This considerable level of individual difference in the suppression duration is one of the characteristics of the interocular suppression phenomenon (Aafjes, Hueting, & Visser, 1966; Carter & Pettigrew, 2003).

To compare the effect of attention between TAE and MAE, we separately conducted three-way ANOVAs on each type of aftereffect. In the case of MAE, where we measured the aftereffect from the visible items, a three-way ANOVA with location, attention, and the presence of the tilted gratings as within-subjects variables was conducted. This analysis revealed that attention increased the amount MAE from 1.07 to 1.67 ($F_{1,11} = 69.657$, $p < 0.01$), as shown in figure 4a (the amount of MAE was calculated as the contrast of the grating drifted toward the MAE direction divided by that drifted toward the adapting direction). These results are consistent with a previous study which showed that spatial attention produced a larger amount of adaptation (Chaudhuri, 1990). However, no other main effects or interactions were significant (all ps > 0.1), and there was no difference in the amount of MAE regardless of whether or not the suppressed adapters were presented. Moreover, the amount of attentional influence on MAE was not influenced by the suppressed adapters. Therefore, the existence of suppressed items does not affect the attentional modulation of the processing of visible items.

For the invisible adapters, we found that spatial attention did not affect the amount of aftereffect (figure 4b). A two-way ANOVA with location and attention as within-subjects variables on TAE showed that there was no significant main effect of either location or attention ($F_{1,11} = 3.600$, $p = 0.84$; $F_{1,11} = 0.003$, $p = 0.959$). Here, the amount of TAE was calculated by repositioning the baseline as each participant's PSE of the vertical orientation. Also, the interaction between the two variables was not significant ($F_{1,11} = 0.467$, $p = 0.509$). These results suggest that spatial attention did not modulate the amount of TAE, in contrast to MAE, despite the fact that the invisible adapters were presented at the same attended location as that used with the visible adapters.

The analysis thus far suggests that the effect of attention changes depending on the visibility of the adapters. To investigate whether the visibility of the adapters is related to the amount of attentional influence, we examined the correlation between the visibility of the tilted adapters and the amount of attentional influence. It should be noted that the visibility of the tilted adapters does not indicate the actual visibility of the adapters during adaptation because it was measured in a separate session. To quantify the amount of attentional influence, we divided the amount of TAE in the attended location by that in the unattended one. We found there was no significant correlation between the visibility of the tilted adapters and the amount of attentional influence ($r_{12} = 0.41$, $p = 0.186$).

Our finding that attention increases the amount of MAE but not TAE may indicate that the resource of spatial attention is more likely to be distributed to visible items than to invisible items. However, it is possible that no effect of attention was found on TAE because the signal strength of the tilted gratings was not strong enough to reflect the attentional modulation. If there was no aftereffect from these adapters, it would be impossible to measure the effect of attention on TAE. We examine this possibility by comparing the amount of TAE after adaptation with each participant's PSE without adaptation. The PSEs (1.056 deg on average) after adaptation significantly differed from the PSE (0.315 deg on average) before adaptation ($t_{11} = -2.274$, $p < 0.05$). Therefore, it is unlikely that our failure to observe an effect of attention on the tilted grating was due to the weak strength of the adapters.

As the effect of attention differed depending on participants' performances on the attention task, we also found a significant correlation between CDD performance and the amount of TAE in the attended locations ($r_{10} = 0.641$, $p = 0.025$). However, there was no significant correlation between the CDD performance and the amount of TAE in the unattended locations ($r_{10} = -0.048$, $p = 0.883$). That is, when participants performed the CDD task better, attention was more likely to influence the processing of the tilted gratings presented at the location where the task was performed. These results suggest that the processing of invisible items can be modulated by spatial attention only when the engagement of attention is sufficient.

The main goal of experiment 1 was to compare the effect of attention between visible and invisible items when spatial attention is focused on a location where these two types of stimuli were presented. We found that visible items were influenced by spatial attention, while invisible items presented at the same location were not. Therefore, it seems that attention gives priority to the processing of visible stimuli while leaving invisible stimuli less affected. However, our results do not suggest that invisible information is not affected by attention. As previous studies also showed (Shin et al., 2009), we found that attention tends to influence the processing of invisible items when attentional engagement reflected in the task performance is relatively high.

Nonetheless, our findings may seem inconsistent with previous studies that showed the effect of attention on the processing of invisible items (Bahrami et al., 2008; Shin et al., 2009). We reasoned that attention may not have significantly modulated the amount of TAE because only dominant items were relevant to the CDD task. Recent studies showed that attention can be triggered in an eye-specific manner (Ooi & He, 1999; Zhang, Jiang, & He, 2012).

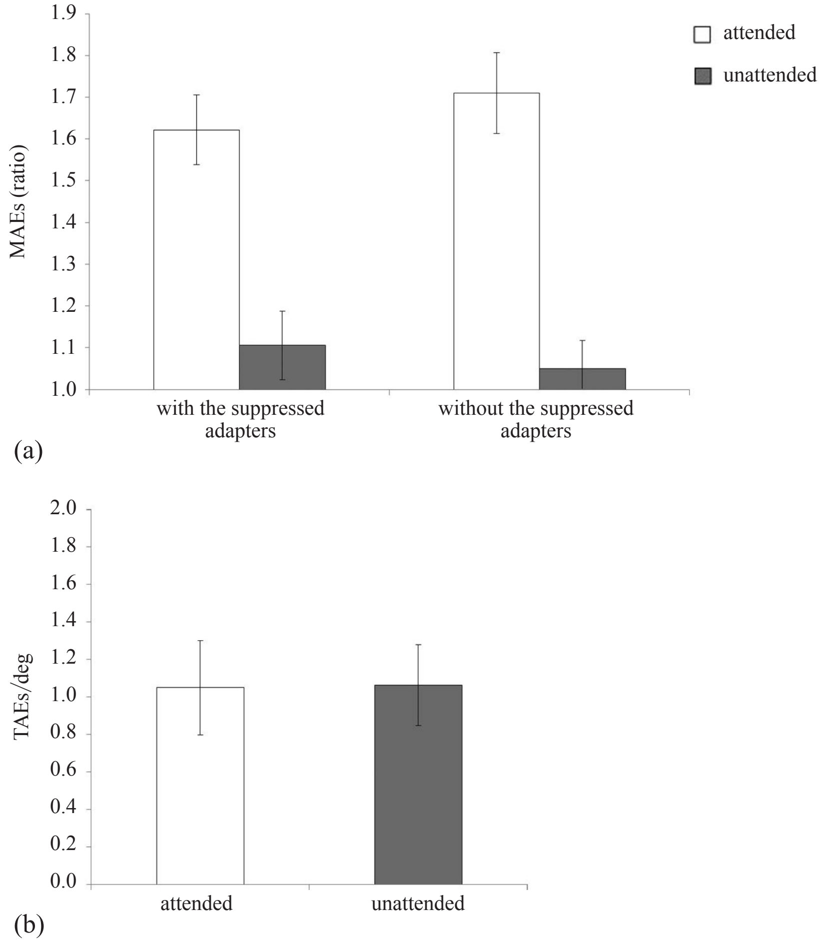


Figure 4. (a) The amount of motion aftereffect (MAE), which was calculated as the contrast of the grating drifted opposite to the direction of the adapters divided by the contrast of the grating that drifted as the same direction of the adapters. (b) The amount of tilt aftereffect (TAE), indicating the difference in the points of subjective equality of the vertical orientation before and after the adaptation.

That is, if attention is modulated by visual input from one eye, information from the other eye is less likely to be affected by attention. Furthermore, in their experiment 1b Zhang et al. (2012) found that, when a monocular cue was presented to an eye to which a mask was presented, the suppression time for the images from the opposite eye became longer compared with when a binocular cue was used. If this is the case, our finding that TAE was not affected by attention can be attributed to the eye-specific effect of attention and not to the visibility of the stimuli. To test this possibility, we adopted a dichoptic task to modulate attention and compared the aftereffects from visible and invisible adapters in experiment 2.

3 Experiment 2

In experiment 2 we used a dot detection task to modulate spatial attention. In this task a dot briefly appeared in both eyes, ensuring that both eye channels were engaged in attention. We believe that this manipulation allows us to investigate whether a monocular change in experiment 1 biased the allocation of attention toward the dominant item.

The orientation of the motion adapters changed, becoming orthogonal to that of the tilted adapters in this experiment. In experiment 1 the motion adapters were vertical, and their direction was either leftward or rightward, overlapping somewhat with the orientation of the tilted adapters. Although we found a significant amount of TAE, the orientation of the motion adapters may still hamper the generation of TAE, as orientation information can be transferred interocularly (Mitchell & Ware, 1974). To rule out this possibility, we altered the orientation of the motion adapters so that they were horizontal and drifted either upward or downward. Finally, we also changed the method used to measure MAE: unlike the contrast ratio of the two directions of motion in experiment 1, in experiment 2 we measured the response bias toward the opposite direction of the MAE adapters. We changed the method because we felt that doing so made it easier for participants to report the percept of direction when the tester has one direction of motion instead of two directions combined. In addition, this strategy could reduce the duration of the experiment.

3.1 *Methods*

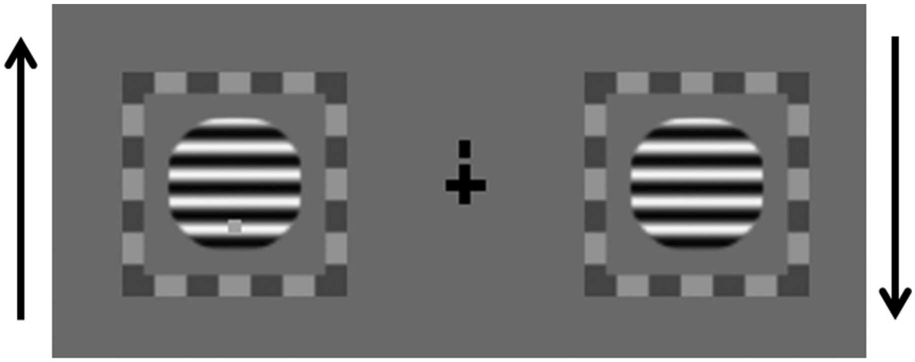
3.1.1 *Participants.* Twelve Yonsei University students, five (including the first author) who had participated in experiment 1 and another seven who were newly recruited, participated in experiment 2. All except the author received a monetary reward for participation. All had normal or corrected-to-normal vision. All except the author were naive to the purposes of the study and gave written informed consent after receiving an explanation of the procedures. Every aspect of this study was approved by the Institutional Review Board of Yonsei University.

3.1.2 *Apparatus and stimuli.* All of the apparatus used in experiment 2 was identical to that used in experiment 1. The stimuli were identical to those used in experiment 1, except for the following differences. First, the direction of the MAE adapters was either upward or downward, and the orientation of the drifting gratings was horizontal. The direction of motion at each location was counterbalanced across participants. Second, the stimulus used to measure MAE was changed. We used a different paradigm based on perceptual bias to measure the amount of MAE (Kaunitz, Fracasso, & Melcher, 2011). We changed the method because we wanted to generalize our results across different methods and reduce the duration of the experiment. The test stimulus was a grating with a contrast of 10% and a spatial frequency of 6 cycles deg^{-1} and which drifted at a speed of 0.027 deg s^{-1}. In the case of the tilted adapters for TAE, all aspects of the stimulus were identical to those in experiment 1. The test stimulus for TAE had the same parameters as those used in experiment 1, but the orientation of the test stimulus differed. We measured each participant's PSE of orientation discrimination and used stimuli that were tilted ±1 deg from each participant's PSE as the test stimuli.

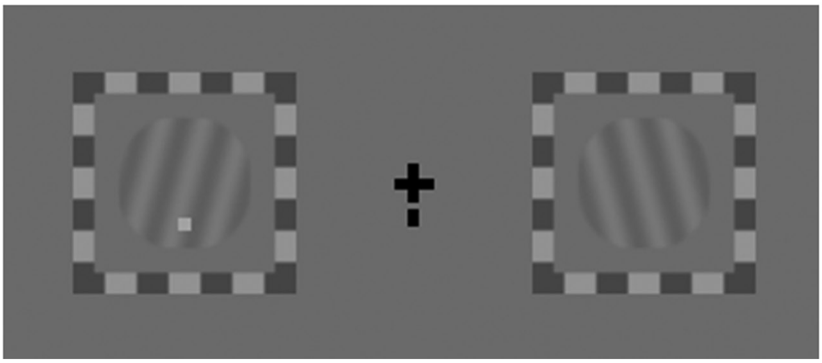
For the dot detection task, we used a dot whose diameter was 0.18 deg. The Weber contrast from the background was 25%. It was presented in the corresponding locations of two eyes and appeared briefly (50 ms) at random intervals.

3.1.3 *Procedure.* Unlike experiment 1, which consisted of three different sessions, in experiment 2 the aftereffects and the visibility of the suppressed stimuli were measured simultaneously. Depending on the task location, there were two blocks to measure TAE. MAE was measured in four different blocks depending on the task location and the existence of the suppressed adapters. Before the main experiment, the PSE of the participants to the vertical orientation was measured in the same manner used in experiment 1 to determine the orientation of the test stimulus for TAE.

Each block started when the checkerboard frame surrounding the adapters flickered, indicating the location where participants had to attend and perform the dot detection task. As the experiment started, two drifting gratings appeared as motion adapters on either side of the central fixation cross. They were presented to the dominant eye in order to increase their probability of being visible. These gratings drifted either upward or downward such that the two adapters had different directions of motion. After 3 s, two tilted gratings gradually appeared in the same locations of the suppressed eye where the motion adapters were presented. The contrast of the tilted gratings was linearly increased for 5 s, from 0% to full contrast, so as not to disturb the temporal dynamics of suppression. The orientation of the tilted adapters was either 15° or –15°. Given that there could be mixed perceptions of these drifting and tilted gratings, participants were instructed to keep pressing the ‘z’ key if they perceived either tilted gratings or a mixture of drifting and tilted gratings. The tilted and drifting gratings disappeared 2 s after the tilted grating reached its full contrast. Therefore, the participants were adapted to motion for 10 s and to orientation for 7 s. While they were adapted to motion and orientation, they performed a dot detection task at the cued location. A dot randomly appeared during the adaptation either twice or three times in both the dominant and nondominant eyes (figure 5). The dot was presented on the adapters for 50 ms, and its location was slightly changed whenever it appeared. Participants were asked to press the ‘2’ key as quickly as possible whenever they detected the dot. There was no feedback for their responses.



(a)



(b)

Figure 5. (a) The motion adapters that drifted either upward or downward. A dimmed dot briefly appeared on the cued side of the grating, and participants were instructed to detect the dot whenever it appeared. (b) The tilted adapters with a dot to be detected; the dot was presented at the corresponding location where it appeared in the dominant eye.

After 10 s of adaptation, MAE and TAE were measured in a separate block. In the MAE case a grating that drifted either upward or downward was presented for 50 ms. It was presented on either the left or right sides of the central fixation cross, and its location was cued by the flicker of the checkerboard frame beforehand. Participants were instructed to report the direction that they had perceived (the ‘8’ key for upward drift and the ‘5’ key for downward drift). The test stimulus moved half of the time in the direction of the adapter and half of the time in the direction opposite to the adaptor. We assumed that if participants were successfully adapted to the motion adapter, biased responses toward the opposite direction of the adapter would arise as a consequence of MAE (Kaunitz et al., 2011).

The amount of TAE was measured with a grating whose parameters, except for the orientation, were identical to those of the tilted adapters. For half of the trials, the orientation of the test stimulus was tilted in the TAE direction; in the other trials, it was in the opposite direction. As in the MAE measurement blocks, participants reported the orientation of the test stimulus by pressing the '6' key for clockwise and the '4' key for counterclockwise. Their bias toward the direction opposite to the adapted orientation was measured as the amount of TAE. Every test trial was followed by a top-up adaptation, which was similar to the initial adaptation period except that drifting gratings were presented for 5 s while tilted gratings gradually appeared from the beginning, reaching their full contrast after 3 s.

3.2 *Results and discussion*

Before analyzing the aftereffects from the visible and invisible adapters, we checked the performance of the dot detection task. The average detectability of the task was 88.7%, with a standard deviation of 7.12%, and there was no difference between the MAE and the TAE blocks ($t_{11} = -0.913$, $p = 0.381$). Therefore, the degrees of attentional modulation on the visible and invisible adapters were similar.

We also tested the visibility of the suppressed adapters. The visibility of the suppressed adapters, which indicates the time during which the participants reported that the suppressed adapters were visible divided by the entire presentation time of the suppressed adapters, was 17.26%, with a standard deviation of 15.69%. There was no difference in the visibility of the suppressed adapters between the TAE and MAE blocks ($t_{11} = 1.32$, $p = 0.214$).

The aftereffects measured in experiment 2 were analyzed by performing ANOVAs in the same manner as in experiment 1. We first analyzed the amount of MAE that was induced by the visible adapters. As in experiment 1, there was a greater amount of MAE in the attended location compared with the unattended location ($F_{1,11} = 11.569$, $p = 0.006$) (figure 6a). Therefore, spatial attention effectively enhanced the amount of adaptation from the visible adapters, as in experiment 1. The effect of attention was relatively strong on the left side of the fixation cross as compared with the right side; the interaction between attention (attended, unattended) and location (left, right) was significant ($F_{1,11} = 5.030$, $p = 0.046$). It should be noted that participants performed the task similarly when attending to either the left or right sides ($t_{11} = 0.375$, $p = 0.714$), although there were greater effects of attention when they attended to the left side. Except for these effects, no other main effect or interaction was significant, as in experiment 1. The amount of MAE did not differ between the two locations ($F_{1,11} = 1.248$, $p = 0.288$), and the presence of the suppressed adapters did not influence attentional modulation of the visible adapters ($F_{1,11} = 3.020$, $p = 0.110$), consistent with experiment 1.

In the case of TAE from the suppressed adapters, we found a marginal trend showing that attention increased the amount of adaptation; there was a slightly higher amount of TAE when the adapter was attended compared with when it was unattended ($F_{1,11} = 3.503$, $p = 0.088$) (figure 6b). These results suggest that the dichoptic cue in experiment 2 attracted spatial attention to the suppressed adapters better than the monocular cue in experiment 1. Nevertheless, given that the effect of attention did not reach a significant level, the influence of attention on the processing of invisible stimuli seemed to be weaker compared with that on visible stimuli. No other main effect or interaction was significant.

To further examine whether the amount of attentional influence is associated with the visibility of the stimulus, we performed a correlation analysis of the amount of attention on TAE and the visibility of TAE adapters. We calculated the amount of attentional influence by dividing the amount of TAE in the attended location by that in the unattended location, as in experiment 1. We found that there was no significant correlation between the amount of attentional influence on TAE and the visibility of TAE adapters ($r_{12} = 0.093$, $p = 0.773$). We then categorized the trials based on the visibility report and investigated whether the amount of attentional influence on TAE differed depending on the degree of visibility. If a participant perceived the TAE adapters longer than 25% of the presentation time in a given trial, the trial was classified as a partially suppressed trial; if it was less than 25%, we defined it as an invisible trial (Moradi, Koch, & Shimojo, 2005). Five of the twelve participants had no partially suppressed trials or invisible trials in any condition and were therefore excluded from this analysis. We found that, for the invisible trials, there was a marginal effect of attention on TAE ($F_{1,6} = 5.596$, $p = 0.056$). For the partially suppressed trials, however, attention significantly increased the amount of TAE ($F_{1,6} = 9.342$, $p = 0.022$). These results indirectly show that the degree of attention varied depending on the visibility of stimuli.

Blake, Tadin, Sobel, Raissian, and Chong (2006) showed that the strength of visual adaptation varies depending on the visibility of the adapters. We found a similar trend in our data; there was a significant correlation between the visibility of the TAE adapters and the amount of TAE ($r_{12} = 0.706$, $p = 0.010$). These findings are in line with findings showing that the amount of adaptation is closely related to the degree of awareness (Stein & Sterzer, 2011).

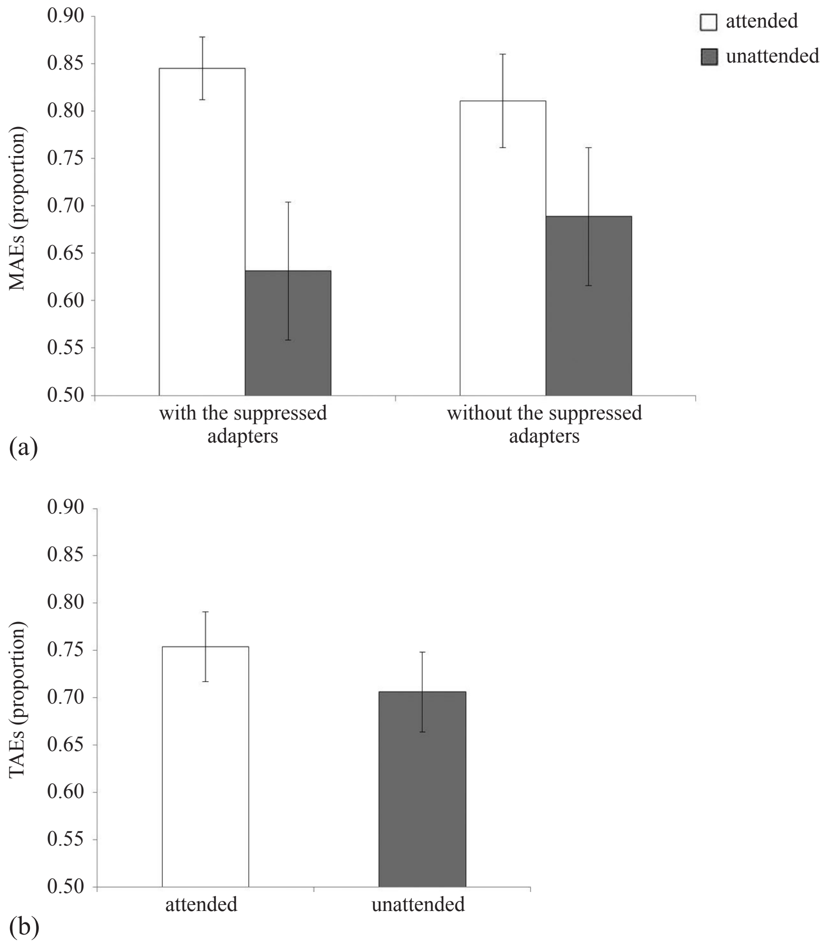


Figure 6. (a) The amount of motion aftereffect (MAE), which indicates the degree of bias toward the MAE direction, and (b) the amount of tilt aftereffect (TAE), which indicates the degree of bias in the TAE direction.

Although there was no correlation between performance on the CDD task and the visibility of the suppressed adapters in experiment 1, we found that the task performance level on the dot detection task was positively correlated with the visibility of the suppressed adapters (r_{10} = = 0.657, $p = 0.02$). This arose because, when attending to the suppressed image in this case, a dot presented to the suppressed eye increases the probability of breaking the suppression (Ooi & He, 1999).

The results of experiment 2 show that a dichoptic cue can, to some degree, attract spatial attention to suppressed adapters. However, the engagement of attention was biased toward the dominant adapters; there was a significant effect of attention on the dominant adapters, whereas it was only marginal on the suppressed adapters. Furthermore, we found that the presence of the suppressed adapters did not interfere with attentional influence on the dominant items, as in experiment 1. These results suggest that, when spatial attention is distributed toward dominant and suppressed items occupying the same location, the dominant items achieve a greater attentional boost compared with the suppressed items.

4 Experiment 3

Experiments 1 and 2 demonstrate that the effect of attention is weaker for the suppressed adapters than it is for the dominant ones. Although the effect of attention on an invisible adapter is weaker due to the interocular suppression, there is another possibility that the TAE itself is not strong enough to reflect the effect of attention.

To validate the procedure used to measure TAE in experiment 2, we measured the effect of attention on TAE without interocular suppression. We predicted that if it is the interocular suppression that removed the attentional boost on the tilted adapters in experiments 1 and 2, there would be a sufficient amount of attentional influence on TAE when the tilted adapters were presented without being suppressed, consistent with a previous study (Spivey & Spirn, 2000).

4.1 *Methods*

4.1.1 *Participants.* Twelve new Yonsei University students participated in this experiment, and all received a monetary reward for their participation. All had normal or corrected-to-normal vision. All of the participants were naive to the purposes of the study, and all gave written informed consent after receiving an explanation of the procedures. Every aspect of this study was approved by the Institutional Review Board of Yonsei University.

4.1.2 *Apparatus and stimuli.* All aspects of the apparatus and the stimuli were identical to those used in experiment 2.

4.1.3 *Procedure.* The procedure of experiment 3 was identical to that of the blocks measuring the TAE in experiment 2, except that there was no moving adapter presented to the dominant eye. Therefore, participants were readily able to see that the tilted adapters gradually appeared from the gray background when they ere adapted to these adapters. As in experiment 2, we measured the PSE to the vertical line for each participant before measuring TAE and used it as the baseline when we calculated the amount of TAE.

4.2 *Results and discussion*

The average detection rate of the dot detection task was 97.5%, with a standard deviation of 2.46. When we compared the performance of the dot detection task in the TAE blocks of experiments 2 and 3, we found that, without moving gratings to the dominant eye, the detection rate was significantly better ($t_{11} = -4.328$, $p = 0.001$).

As in experiment 2, we performed a three-way ANOVA with attention and task location as within-subjects variables to assess how attention influenced the amount of TAE. We found, unlike in experiment 2, that there was a significant difference in the amount of TAE between the attended (82.60%) and unattended locations (69.38%) ($F_{1,11} = 9.201$, $p = 0.011$) (figure 7). These results suggest that, without the suppressors, the tilted adapters were effectively influenced by spatial attention. Finally, neither the main effect of task location ($F_{1,11} = 0.599$, $p = 0.455$) nor the interaction between task location and attention ($F_{1,11} = 0.850$, $p = 0.376$) was significant. These findings suggest that, without the dominant adapters, the amount of TAE was successfully modulated by spatial attention.

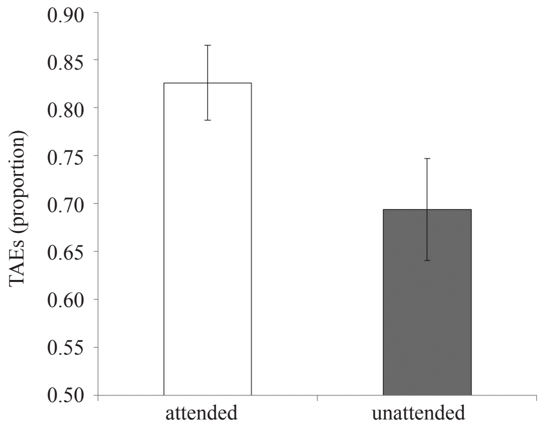


Figure 7. The amount of tilt aftereffect (TAE), as measured without the dominant adapters.

We compared the amount of TAE in the unattended locations between experiments 2 and 3. If there are equivalent amounts of TAE in the unattended locations of the two experiments, it can be inferred that it is not the aftereffect itself but interocular suppression that led to the different results between the two experiments. We found that the amount of TAE in the unattended location did not differ depending on the presence of dominant adapters (experiment 2: 70.63%, experiment 3: 69.36%; $t_{11} = 0.244$, $p = 0.812$). Therefore, the differences in attentional influence on TAE between the two experiments are due to the interocular suppression from the dominant adapters.

In sum, we examined the effect of attention on the TAE when the adapters were visible with the same procedure used in experiment 2. Unlike experiment 2, we found that our manipulation of attention successfully increased the amount of TAE when the tilted adapters were not suppressed. These findings suggest that the relatively weak effect of attention on TAE in experiment 2 arose due to the interocular suppression of the tilted adapters and not due to the procedure used in experiment 2.

5 General discussion

The present study investigated the distribution of attentional influence on the processing of visible and invisible items under binocular competition. In three experiments we examined how attention influenced the amount of adaptation as induced by the visible and invisible adapters. The adapters were located on the left and right sides of a central fixation cross, and participants performed a task that directed their spatial attention to one side. In experiment 1 the task was to detect the decrement of the contrast on drifting gratings, while the task of experiment 2 was to detect a dot presented in both eyes. We found that attention was induced by either a monocular change (experiment 1) or a binocular cue (experiment 2); attention mainly influenced the visible adapters, whereas the effect of attention was minimal for the invisible adapters. We also found that the amount of attentional modulation was not affected by the presence of suppressed items. Finally, we show that the relatively weak effect of attention on the suppressed adapters did not originate from the insufficient amount of the TAE, because when these adapters were not suppressed, attention effectively increased the amount of TAE.

Ling and Blake (2012) proposed the normalization model of binocular rivalry. In their study they showed that, when the attentional field is small, a response gain shift occurs and the dominant item achieves priority of attentional influence over the suppressed item. The present study supports this by showing the same trend in the results with different types of aftereffects. Along with this model, several studies have recently suggested that attention is a key factor in the inequality of the signal strength levels of two competing images (Brascamp & Blake, 2012; Zhang, Jamison, Engle, He, & He, 2011). For example, Brascamp and Blake (2012) showed that, when voluntary attention is allocated to a location unrelated to rival images, the dynamics of binocular rivalry is abolished, as though the images do not compete with each other. According to these researchers, attention biases the conflict between two images by amplifying the benefits that one representation has over the other under rivalry. Dieter and Tadin (2011) also suggested that attention intensifies the differences between the strength of competing items under binocular rivalry by biasing the attentional boost in favor of the dominant item. Our findings support this perspective, showing that attention differentially influences two competing images. As the dominant item is more strongly modulated by attention, the discrepancy concerning the strength of the two images can be exaggerated, which is critical to initiate rivalry between images.

Although the effect of attention on the processing of suppressed items is weak, we found that it depends on how attention is induced; the suppressed adapters in this study were somewhat influenced by attention when a dichoptic cue was used to modulate spatial attention (in experiment 2), but this was not the case with a monocular cue (experiment 1). These discrepant findings occurred because the effect of voluntary attention is greater on information from an attended eye. According to Zhang et al. (2012), the effect of top-down attention can be eye-specific because attentional modulation is found in the early stages of visual processing, where the information from each eye is kept separate in each eye channel. In other words, the amount of attentional modulation on a visual stimulus can depend on the eye of origin of the attended image. Supporting this perspective, Chong, Tadin, and Blake (2005) showed that attending to one image under binocular rivalry lengthened the dominant duration of the attended image while leaving the dominance duration of the unattended image unchanged. Our findings are consistent with this study because attention influenced suppressed items only when an attentional cue was presented to the suppressed eye.

Our findings, which showed no effect of attention on suppressed adapters, may seem at odds with previous studies that found that attention can influence the processing of suppressed items (Bahrami et al., 2008; Shin et al., 2009). We believe that the discrepancy between the present study and earlier findings can be attributed to several reasons. First, unlike previous studies that used random masks to render adapters invisible, the dominant adapters in the present study were gratings that drifted in a coherent direction. For masks with random noise, there is no specific information that attention can engage. Therefore, attention is more likely to be distributed to the suppressed items in these studies, which in turn allows attention to facilitate the processing of suppressed items, as previous studies have shown. However, the drifting gratings that we used as dominant stimuli included direction information, for which visual processing can be boosted by attentional modulation. Therefore, in our experiments attentional influence may have been more exclusively allocated to dominant items. The considerable amount of attentional modulation on MAE in both experiments 1 and 2 supports our hypothesis. Second, the types of aftereffects measured by invisible adapters in the present study were different from those in previous studies. In both Bahrami et al. (2008) and Shin et al. (2009) the aftereffects from invisible adapters were measured using the contrast of the stimuli. In the present study, however, we measured TAE, which is related to the orientation of the adapters. According to Festman and Ahissar (2004), the contrast of stimuli is more sensitive to spatial attention than to orientation. Therefore, it is possible that TAE as employed in the present study was not sufficiently sensitive for spatial attention to reflect its subtle influence on the invisible adapters. Supporting our assumption, Kanai et al. (2006) also did not find an effect of spatial attention on invisible adapters when measuring TAE. Finally, although we directly compared the amount of attentional influence on MAE with that on TAE, it should be noted that there are differences in the two types of adaptation. It is known that attention exerts different amounts of influence depending on various stages of visual processing; the higher the visual processing stage, the more likely it is to be modulated by attention (Kastner & Ungerleider, 2000). In the present study both of the measured aftereffects were processed early in visual processing, but not at the same stage; orientation is known to be processed at an early stage, such as V1 (Hubel & Wiesel, 1968), while first-order motion is processed during MT as well as V1 (Mikami, Newsome, & Wurtz, 1986; Snowden, Treue, Erikson, & Anderson, 1991). Because the processing of motion is related to relatively high areas compared with those associated with orientation processing, it is possible that the drifting gratings were comparably more vulnerable to attentional modulation. However, given that the processing of orientation can be influenced by spatial attention when there is no interocular suppression (in experiment 3), our findings still suggest a biased amount of attentional modulation on dominant items at the expense of the impact on the suppressed items.

In sum, the present study examined how spatial attention is allocated to visible and invisible items under binocular competition. Although previous studies have found that attention can affect the processing of suppressed, and thereby invisible, items under interocular competition (Bahrami et al., 2008; Shin et al., 2009), our data suggest that the amount of attentional influence on the suppressed items is relatively weak compared with that on the dominant items. Furthermore, the suppressed items do not interfere with the attentional influence on the dominant items, as the amount of attentional boost on the visible adapters did not differ depending on the presence of suppressed adapters. These findings suggest that attention biases the strength of two competing items by preferentially benefiting the dominant items, which enables competition between two different images presented to each eye.

Acknowledgments. This research was supported by the Basic Science Research Program through the National Research Foundation of Korea funded by the Ministry of Education, Science and Technology (2011-0025005) of Korea.

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