Attentional modulation of adaptation to illusory lines

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Selective visual attention modulates neuronal activation in various cortical areas. This type of neuronal modulation could happen even in the early stages of visual processing where specific attributes of visual stimuli are processed. It has been shown that different forms of visual aftereffects, such as tilt aftereffect, motion aftereffect, and figural aftereffect, are modulated by attention. In this study, we investigated the effect of visual attention on adaptation to illusory lines. In the first experiment, orientation selective adaptation to a peripheral illusory line was measured in three conditions: (1) poor attention condition in which subjects performed a dual task (even-odd judgment) at the fixation point during the adaptation period, (2) partial attention condition in which subjects only observed successively presented digits at the fixation point and did not perform the task during the adaptation period, and (3) full attention condition in which no visual stimuli were presented at the fixation point. Results showed that the magnitude of adaptation systematically decreased as the attentional load at the fixation point increased. In the second experiment, two transparent illusory contours were presented during the adaptation period, and tilt aftereffects to attended and non-attended illusory lines were compared. The magnitude of tilt aftereffect to the attended illusory line was significantly greater than that to the non-attended illusory line even when non-attended illusory contour was more visually salient. Because visual areas V2 and V1 are the first stage in the processing of illusory contours, we could conclude that visual attention has modulatory effects on the activation of neurons in these areas.

Keywords: orientation selective adaptation, tilt aftereffect, illusory line, attention, early visual cortical areas

Introduction

Visual attention can be directed to a particular region of space, visual feature, or object, and can enhance the neural processing of attended stimuli and suppress the processing of irrelevant stimuli. Electrophysiological and fMRI studies have revealed the effects of attentional modulation in lateral geniculate nucleus (LGN) of thalamus (O'Connor, Fukui, Pinsk, & Kastner, 2002), primary visual cortex (V1) (Ito & Gilbert, 1999; Motter, 1993; Roelfsema, Lamme, & Spekreijse, 1998), and several extrastriate cortical areas, such as V4 (Moran & Desimone, 1985), V5 (Treue & Maunsell, 1996; O'Craven, Rosen, Kwong, Treisman, & Savoy, 1997), and inferior temporal cortex (Tanaka, Onoe, Tsukada, & Fujita, 2001).

Attentional modulation could happen even in the early stages of visual processing where specific attributes of visual stimuli are processed. Several psychophysical studies have shown that adaptation to different attributes of visual stimuli is modulated by attention. Attention has modulatory effects on the motion aftereffect (Chaudhuri, 1990; Lankheet & Verstraten, 1995; Rees, Frith, & Lavie, 1997), figural aftereffect (Shulman, 1992; Suzuki, 2001; Yeh, Chen, DeValois, & DeValois, 1996), and tilt aftereffect (TAE) (Spivey & Spirn, 2000). However, contrast adaptation remains unchanged in the conditions of inattention (Festman & Ahissar, 2003).

Spivey and Spirn (2000) showed that direct TAE is modulated via selective visual attention. They generated spatially separate or transparent gratings and measured the TAE for attended region compared to unattended region in the spatially separate condition and for attended stimulus compared to unattended stimulus in the transparent condition. Their results demonstrated an effect of voluntary spatial attention and voluntary object-based attention on the TAE that is believed to take place in primary visual cortex (V1) (Wenderoth, van der Zwan, & Johnstone, 1989).

The effect of visual attention on adaptation to gratings (TAE) is a typical example of attentional modulation in early visual areas. Illusory contours are another type of visual stimuli, which are processed at early stages of visual hierarchy. Two line gratings abutting each other with a phase shift elicit the perception of an illusory line between the two sets of grating lines (Soriano, Spillmann, & Bach, 1996). Neurophysiological experiments have shown that illusory contours may be represented at relatively early stages in the visual system such as areas V2 (Peterhans & von der Heydt, 1982; von der Heydt, Peterhans, & Baumgartner, 1984) and V1 (Grosof, Shapley, & Hawken, 1993; Sheth, Sharma, Rao, & Sur, 1996). Occasionally, the responses of V2 neurons to an illusory contour stimulus are even stronger than to a real contour of the same orientation (Baumgartner, von der Heydt, & Peterhans, 1984). It has been shown that the TAE also occurs for illusory contours (Paradiso, Shimojo, & Nakayama, 1989). A question

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that arises here is whether attention can modulate adaptation to illusory lines. Attentional modulation of adaptation to illusory lines may indicate the effects of attentional modulation in early visual cortical areas.

Pritchard and Warm (1983) showed, using a dual task paradigm, that perception of subjective contours (illusory contours) entails a greater attentional demand than that of real contours. In the primary task, subjects made speeded same-different discriminations of either subjective figures or real figures. This task was performed alone or in conjunction with a secondary, short-term memory load task. The presence of the secondary task produced a greater increment in reaction time for subjective than for real figures. On the contrary, there is some evidence implying that an early, parallel, reflexive mechanism is involved in the processing of illusory contours (subjective contours) and thereby, in certain situations, selective attention is unnecessary for encoding the orientation of subjective contours. Gurnsey, Humphrey, and Kapitan (1992) have shown that a target illusory contour can be detected in a visual search task independent of the number of nontarget distractors. Subsequently Davis and Driver (1994) have also reported that even Kanizsa subjective figures can be detected in a visual search task without focal attention at parallel stages of the human visual system. In abovementioned experiments, parallel (preattentive) processing is taken to index processing without attention. However, there is some evidence showing that a preattentive task is impaired when a competing task must be performed in parallel (Di Lollo, Kawahara, Zuvic, & Visser, 2001; Joseph, Chun, & Nakayama, 1997). Dual task procedures have demonstrated that even preattentive feature search tasks need attentional resources. Thus, parallel detection of illusory contours in visual search tasks does not necessarily indicate processing without attention.

Evaluating the effects of attention on adaptation to illusory lines could precisely address the question if attention is necessary for the processing of illusory contours. We investigated the effects of visual attention on orientation selective adaptation to illusory lines (Experiment 1) and illusory line-TAE (Experiment 2). The specific roles of spatial attention and object-based attention were studied in Experiments 1 and 2, respectively. The results showed that both types of attention have modulatory effects on adaptation to illusory lines.

General methods

Subjects

Five observers, three males and two females, aged between 20-25 years, participated voluntarily in the experiments. All subjects were trained psychophysical observers with normal or corrected-to-normal vision. They, however, were naive with respect to the purpose of the experiment.

Apparatus

The stimuli and psychophysical experiments were programmed in Delphi 6 on a Pentium III 800-MHz PC running Windows 2000. Images were displayed on a RGB color monitor, 800 H x 600 V pixel resolution at 60-Hz frame rate (795FT Plus, LG; Korea). The observers were placed in a dark room and viewed displays binocularly while their heads were fixed on a chin and forehead rest. The viewing distance was 50 cm. Data was analyzed using SPSS V.11.

Experiment 1

In this experiment, orientation selective adaptation to illusory lines was compared in full attention, partial attention, and poor attention conditions. In full attention condition, a peripheral patch containing an illusory line (illusory contour) was presented during the adaptation period. To draw attention away from peripheral stimulus, subjects performed a dual task (even-odd judgment) at the fixation point (poor attention condition). In some trials subjects observed only successively presented digits at the fixation point and did not perform the task during the adaptation period. Attentional status in these trials was considered as partial attention condition. The paradigm used in this experiment can address the question if spatial attention has a role in adaptation to illusory lines.

Stimuli

The illusory contours consisted of two line gratings (both oriented either 45° or 135°) abutting each other with a phase shift (abutting gratings). There was an illusory vertical or horizontal border between the two sets of gratings in each grating patch. Each patch subtended 2.86 deg of visual angle and had 4 real lines with 0 deg of tilt angle (angle between two line gratings) and 0 deg of lateral alignment (the amount of lateral misalignment between two line gratings). Line spacing (distance between two lines in each grating) was 0.45 deg and line width was 0.11 deg.

Digit stimuli were numbers from 2 to 9 and about 0.22 x 0.57 deg in size. The color of digits was either black or white.

Procedure

We designed a paradigm to study the orientation selective adaptation to illusory lines (Rajimehr, Montaser-Kouhsari, & Afraz, 2003). Displays used in this experiment are shown in Figure 1. Each trial began with the presentation of a fixation point for 800 msec followed by 4 s of adapting stimulus presentation (adaptation phase), followed immediately by the test stimulus presentation for 580 msec (test phase), and ended with a 2-s period of blank screen as inter-trial interval. In our previous study, we observed that orientation selective adaptation to illusory lines was robust even with a short time period of adaptation (i.e.,

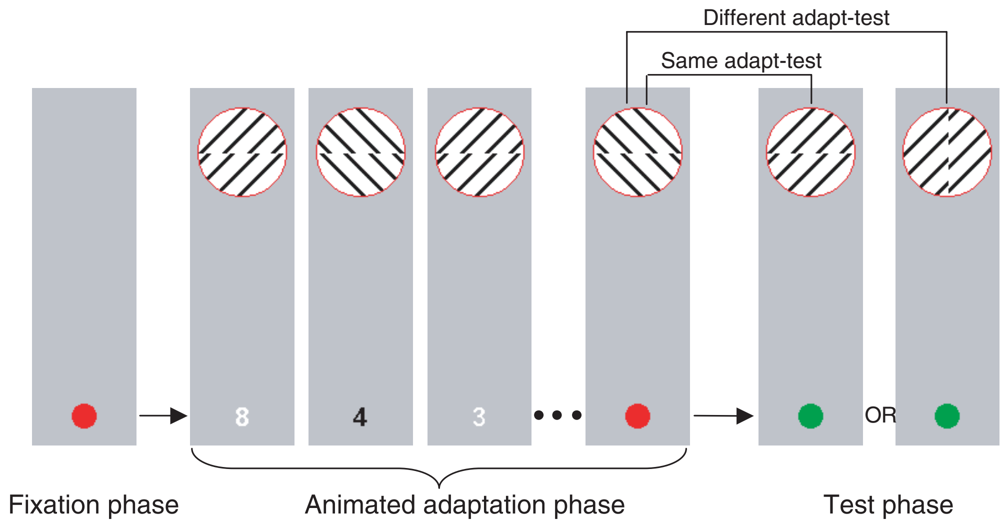

Figure 1. Schematic diagram demonstrating the temporal succession of visual stimuli in a typical trial of the first experiment. Each trial consisted of three phases: fixation phase, animated adaptation phase, and test phase. Adapting and test stimuli were abutting gratings presented above the fixation point. Durations of adaptation and test phases were 4 s and 580 msec, respectively. The fixation point was a small red dot during the adaptation phase that turned green in the test phase. Digit stimuli were presented at the fixation point throughout the adaptation phase except the last 500 msec of this phase. The orientation of the test illusory line was either the same or different from that of the adapting illusory line.

4 s) (Rajimehr, Montaser-Kouhsari, & Afraz, 2003). Adapting and test stimuli were abutting gratings presented 8.5 deg above the fixation point. The fixation point was a small red dot during the adaptation phase that turned green in the test phase. Observers were asked to fixate on the fixation point, maintain their fixation through the trial and report the orientation of the illusory line in the test patch (appearing in the periphery of their visual field) at the end of each trial.

Because we intended to study the pure adaptation to illusory lines, orientation specific adaptation of the real grating lines should be avoided as well as retinal adaptation. To rule out the effects of lower level adaptations, an animated stimulus display was used in the adaptation phase. In this animation, the orientation of real lines inside the adapting patch changed to orthogonal orientation repeatedly (7 times in every 4 s of the adaptation phase), but the orientation of illusory lines remained the same (see Figure 1). As a result, there was no adaptation to real lines while our stimuli could still induce the perception of illusory lines with constant orientations during the 4 s of adaptation phase. The orientation of adapting illusory line was chosen randomly (either vertical or horizontal).

The test stimulus was presented after the animated adaptation phase. It was placed at the same location as adapting stimulus (see Figure 1). The orientation of the test illusory line was either the same or different from that of the adapting illusory line.

Subjects were asked to report the orientation of the test illusory line (while fixating on the fixation point) by pressing one of the two alternative keys on the computer keyboard.

There were three attentional conditions during the adaptation period. In full attention condition, no stimulus was presented at the fixation point and subjects were instructed to covertly attend to the adapting stimulus.

In poor attention condition, a stream of randomly chosen black or white digits appeared at the fixation point with the frequency of 2 Hz. Subjects were asked to make even-odd judgments for each black digit presented in the stream by pressing one of the two alternative keys on the computer keyboard. Trials where the average performance (percentage correct) of the digit task was below 75% were excluded in data analysis. No digit stimuli were presented at the fixation point during the last 500 msec of the adaptation phase and a red dot appeared instead. Removal of digit stimuli in the last 500 msec of the adaptation phase enabled subjects to easily disengage their attention from the fixation point and get ready for orientation discrimination of the test illusory line.

In partial attention condition, the stream of digits was presented at the fixation point during the adaptation period but subjects only attended to digits and did not perform the task. Like the previous condition, the digit stimuli were not presented during the last 500 msec of the adaptation phase.

A text cue was presented at the beginning of each trial (during the presentation of fixation point) that determined which attentional condition would be presented.

Each subject completed 5 blocks, each containing 50 trials counterbalanced for the attentional condition, the orientation of adapting stimulus and the orientation of test stimulus.

To quantify the attentional load in the three attentional conditions (full attention, partial attention, and poor attention conditions), we designed another experiment. In this experiment each trial began with the presentation of a fixation point for 800 msec followed by 4 s of blank presentation. An abutting grating was presented for 500 msec in the blank period, 8.5 deg above the fixation point (in the same location as stimuli of the previous experiment). The onset of the stimulus presentation was randomized across trials. The inter-trial interval was 2 s. Observers were asked to fixate at the fixation point and report the orientation of the illusory line in the stimulus patch at the end of trial by pressing one of the two alternative keys on the computer keyboard. Like the previous experiment, there exist three attentional conditions and a text cue was presented at the beginning of each trial (during the presentation of fixation point) that determined which attentional condition would be presented. Each subject completed 5 blocks, each containing 50 trials counterbalanced for the attentional condition and the orientation of illusory line in the stimulus.

Results

We defined two adaptation conditions named same adapt-test where adapting and test illusory lines had the same orientations and different adapt-test. Percentage correct of different adapt-test was significantly more than same adapt-test in full attention condition ($p < .05$ using two tailed t test). It means that the orientation discrimination of the test illusory line in the full attention condition is more accurate when the orientations of adapting and test illusory lines are orthogonal than they are the same (Figure 2). This finding demonstrates robust orientation selective adaptation to the illusory line in the full attention condition.

Difference between percentage correct of different adapt-test and same adapt-test was not significant in the two other attentional conditions (borderline p value, $p \sim .05$, for partial attention condition and $p > .05$ for poor attention condition). It means that orientation selective adaptation to the illusory line is attenuated in partial attention condition and is nearly removed in poor attention condition (see Figure 2).

The overall performance (i.e., average percentage correct of same adapt-test and different adapt-test) in full attention, partial attention, and poor attention conditions was 73.56%, 75.04%, and 74.70%, respectively. There was no significant difference between overall performances in the three attentional conditions ($p > .05$ using one-way ANOVA).

In the experiment of attentional load, the performance of subjects in illusory line-orientation discrimination was quite high in full attention condition and systematically impaired in partial attention and poor attention conditions (Figure 3). In poor attention condition, the performance was not significantly different from the chance level (50%) ($p > .05$ using two-tailed t test). This result demonstrates that a high amount of attentional load at the fixation point exists for poor attention condition and this load decreases in partial attention condition and is minimized in full attention condition. In other words, the magnitude of attention to the peripheral adapting patch is maximal in full attention condition.

The adaptation index could be defined as difference between percentage corrects of different adapt-test and

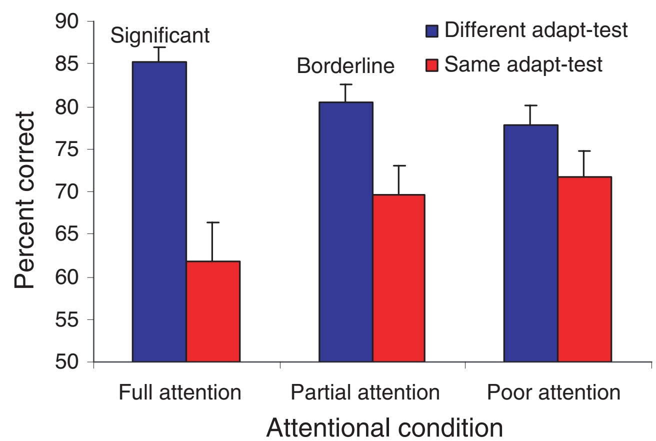

Figure 2. There were two adaptation conditions in Experiment 1: same adapt-test where adapting and test illusory lines had the same orientations and different adapt-test. Percentage correct of different adapt-test was significantly more than same adapt-test in full attention condition. Difference between percentage correct of different adapt-test and same adapt-test was not significant in partial attention and poor attention conditions. Error bars represent 1 SEM.

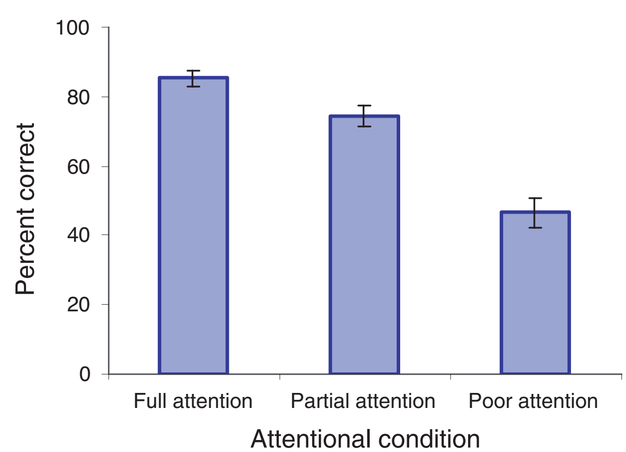

Figure 3. Results of attentional load experiment. The performance of subjects in illusory line-orientation discrimination was quite high in full attention condition and systematically impaired in partial attention and poor attention conditions. Error bars represent 1 SEM.

same adapt-test. There was a significant positive correlation between adaptation index and magnitude of attention to the peripheral adapting patch in three attentional conditions ($r = 0.961$ using Pearson correlation coefficient, $p < .05$ using t test).

Experiment 2

In this experiment, we investigated the effect of visual attention on the TAE to illusory lines in an object-based attention paradigm. In this paradigm, two transparent stimuli (abutting gratings) were presented during the adaptation period. Each stimulus had an illusory line induced by two horizontal or vertical line gratings. The illusory lines were slightly tilted from vertical or horizontal. Because real lines had no tilt from horizontal or vertical, adaptation to real lines would have no effects on TAE to the illusory lines. The color and the orientation of line gratings in the two transparent stimuli were different so that observers could easily focus attention (i.e., object-based attention) on each transparent stimulus (illusory contour) (Ricciardelli, Bonfiglioli, Nicoletti, & Umilta 2001). The TAE was measured for attended and non-attended illusory lines. The comparison between amounts of TAE in the two conditions could show whether the illusory line-TAE is attention dependent or not.

In the second part of this experiment, we decreased the opacity of attended illusory contour and increased that of non-attended stimulus in the transparency condition. Although attended illusory line was less physically salient, it might still have stronger TAE than non-attended illusory line due to attentional modulations.

Stimuli

Each abutting grating contained an illusory line (tilted 15-deg clockwise or 15-deg counterclockwise from vertical or horizontal) induced by two horizontal or vertical line gratings abutting each other with maximal phase shift (180°). Horizontal line gratings elicited an illusory line tilted from vertical and vice versa. The color of line gratings was either green or red. These two colors were isoluminated using heterochromatic flicker photometry (Ives, 1912; Wagner & Boynton, 1972). Like Experiment 1, the diameter of the stimulus patch (abutting grating) was 2.86 deg of visual angle. Each colored line grating had 4 lines with 0 deg of tilt angle and 0 deg of lateral alignment. Line spacing was 0.45 deg and line width was 0.11 deg.

To make a transparent stimulus, two abutting gratings were generated with 50% opacity (red and green gratings were maintained equiluminant) and then superimposed on each other. The line gratings of two transparent abutting gratings were always orthogonal and had different colors (Figure 4A). The two illusory lines in the transparent stimulus were tilted either in the same direction (e.g., both clockwise) or different directions (e.g., one clockwise and the other counterclockwise) (Figure 5). Transparent stimuli were used in the adaptation phase.

Test stimuli were abutting gratings, each containing an illusory line (either vertical or horizontal) induced by two horizontal or vertical black line gratings abutting each other with 180° phase shift. Test stimuli were presented in the test phase.

In the second part of Experiment 2, the opacity of one illusory contour (abutting grating) was 25% in the transparency condition (attended stimulus) and the opacity of the other illusory contour was 75% (non-attended stimulus) (Figure 4B). As a result, red and green gratings had different brightness in this transparency condition.

Procedure

The paradigm we used to study the illusory line-TAE has been shown in Figure 6. Each trial began with the presentation of a text cue (either the word of red or green) in the center of display for 1000 msec. This cue determined the color of line gratings and their related illusory line in

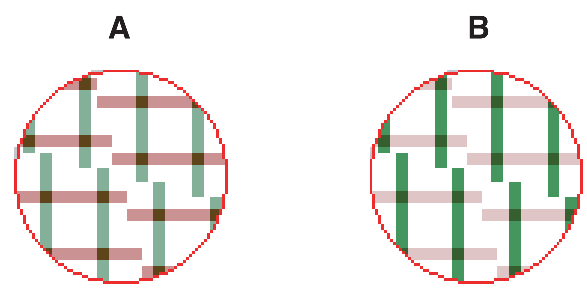

Figure 4. Two examples of stimuli used in the adaptation phase of the first part (A) and the second part (B) of Experiment 2. A. Two abutting gratings (illusory contours) were generated with 50% opacity and then superimposed on each other. B. The opacity of one illusory contour (abutting gratings with red real lines) was 25% in the transparency condition and the opacity of the other illusory contour (abutting gratings with green real lines) was 75%.

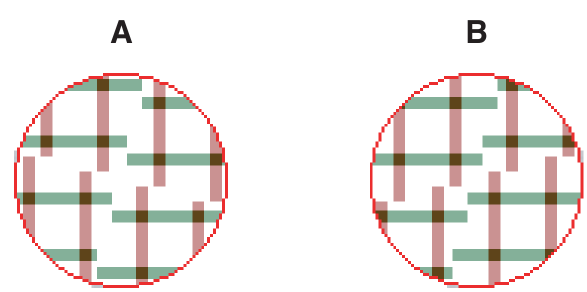

Figure 5. The two illusory lines in the transparent stimulus were tilted either (A) in the same direction – "same tilt stimuli" (e.g., both clockwise) or (B) different directions – "different tilt stimuli" (e.g., one clockwise and the other counterclockwise).

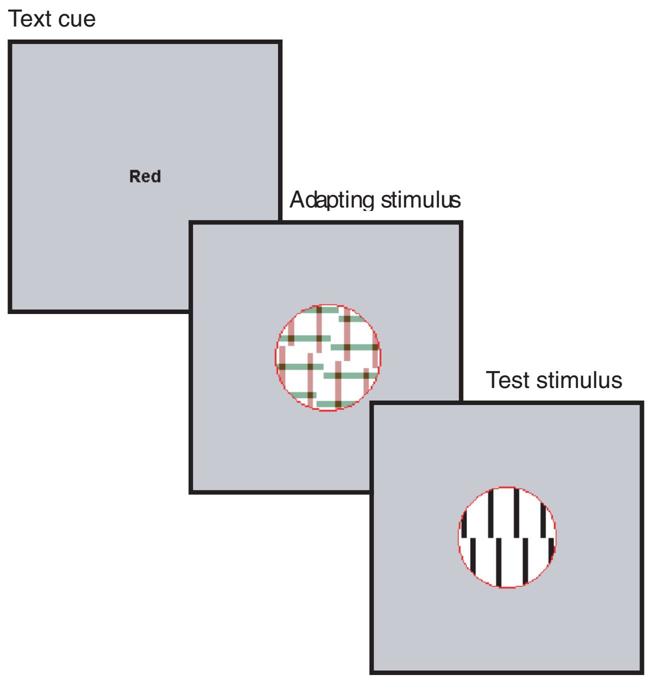

Figure 6. The paradigm of illusory line-tilt aftereffect (TAE) used in Experiment 2. Each trial consisted of three phases: cueing phase, adaptation phase, and test phase. The text cue (e.g., the word of red) determined the color of line gratings and their related illusory line in the transparent stimulus to which subjects should attend through the adaptation phase. A transparent stimulus was presented in the center of display in the adaptation phase and subjects actively attended to the cued illusory contour in the transparency condition. After 30 s, test stimuli (abutting gratings with vertical or horizontal illusory lines) were presented in the same location as adapting stimuli for 1000 msec.

the transparent stimulus to which subjects should attend through the adaptation phase. Adaptation phase began immediately after disappearance of the text cue and lasted 30 s. A transparent stimulus was presented in the center of display in the adaptation phase and subjects actively attended to the cued illusory contour in the transparency condition. After 30 s, test stimuli were presented in the same location as adapting stimuli for 1000 msec. The orientation of test illusory line was selected randomly (either vertical or horizontal). Inter-trial interval was 2 s and observers were asked to report tilt direction of the test illusory line (either clockwise or counter clockwise) by pressing one of two alternative keys on the computer keyboard.

The second part of Experiment 2 was identical in all respects to the previous experiment except that two transparent stimuli with different opacities were presented in the adaptation phase (see Figure 6). The text cue always indicated the color of low-opacity stimulus (i.e., attended stimulus) in the transparency condition.

Results

Classical TAE paradigms have shown that vertical gratings look as slightly tilted clockwise (direct TAE) and horizontal gratings look as barely tilted counterclockwise (indirect TAE) following prolonged viewing of a grating (in the same region of the visual field) slightly tilted counterclockwise from vertical (Gibson & Radner, 1937; Morant & Harris, 1965). Paradiso et al. (1989) have reported TAE for subjective (illusory) contours.

There were two types of trials in our experiment: attended and non-attended. The orientation of test illusory line (either vertical or horizontal) determined the attentional condition. In the attended condition, the test illusory line had an orientation from which the attended illusory line in the adapting stimulus was tilted (e.g., test illusory line was vertical, attended illusory line was tilted from vertical, and non-attended illusory line was tilted from horizontal). In the non-attended condition, the non-attended illusory line in the adapting stimulus was tilted from the test illusory line. Results showed that direct illusory line-TAE was robust only in the attended condition. A minimal but not significant direct TAE to illusory lines occurred in the non-attended condition (Figure 7). Difference between magnitudes of TAE in the two conditions was significant ($p < .05$ using two-tailed t test).

The two illusory lines in the transparent stimulus could be tilted in the same direction –same tilt stimuli (e.g., both clockwise) or different directions – different tilt stimuli (e.g., one clockwise and the other counterclockwise). Same tilt means that the illusory contours were 90 deg different from each other, and different tilt means they were 60 deg apart. We also measured the direct TAE to illusory lines for separate groups of same tilt stimuli and different tilt stimuli. Figure 8 shows the magnitude of direct TAE to attended and non-attended illusory lines for same tilt stimuli

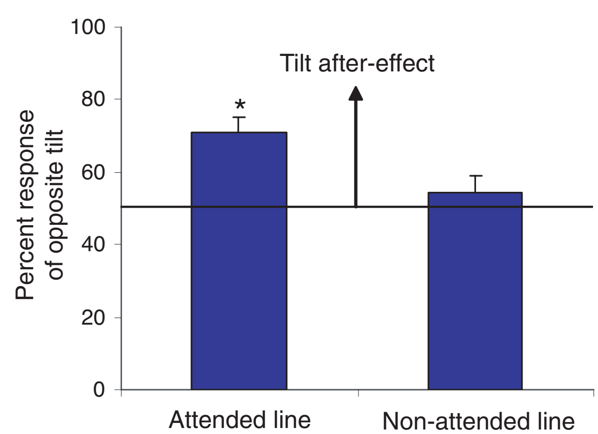

Figure 7. Direct TAE to illusory line was defined as the percentage of trials where the perceived tilt of the illusory line in the test stimuli was in opposite direction to the illusory line's tilt in the adaptation period. Direct illusory line-TAE occurred only in the attended condition. Error bars represent 1 SEM.

and different tilt stimuli. In same tilt stimuli, the magnitude of direct TAE was considerably high in the attended condition ($p < .05$ using two-tailed t test), whereas TAE was absolutely removed in the non-attended condition ($p > .05$ using two-tailed t test). As will be discussed later, this analysis could show if both direct and indirect illusory line-TAEs are modulated by attention.

In the second part of Experiment 2, direct TAE in attended condition was significantly greater than that in non-attended condition ($p < .05$ using two-tailed t test), although the attended stimulus had less opacity than the other stimulus (Figure 9).

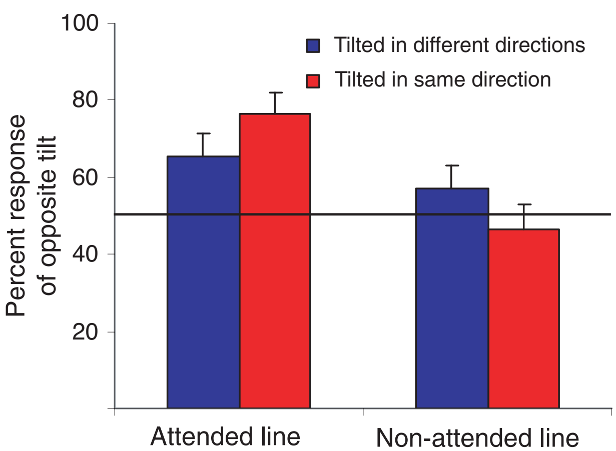

Figure 8. The magnitude of TAE to attended and non-attended illusory lines for same tilt stimuli and different tilt stimuli. Error bars represent 1 SEM.

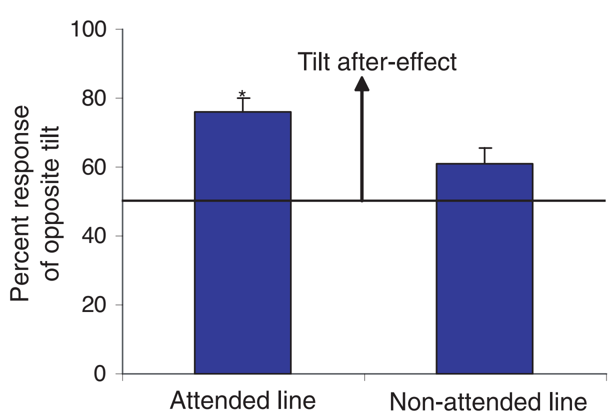

Figure 9. Results of the second part of Experiment 2. Direct TAE in attended condition was significantly greater than that in non-attended condition, although the attended stimulus had less opacity than the non-attended one. Error bars represent 1 SEM.

Discussion

Orientation selective adaptation to illusory lines decreased in the presence of a competing task, which must be performed in a spatially separate location. This result shows that spatial attention modulates orientation selective adaptation to illusory lines. There was a systematic change in the adaptation index of different attentional conditions (full, partial, and poor attention conditions). More attentional load in the fixation point leads to less adaptation to the illusory line presented in a peripheral patch. This shows the modulatory effect of spatial attention on this type of adaptation.

In full attention condition, the subjects were instructed to fixate at the fixation point and covertly attend to the adapting stimulus. We did not monitor eye position in this condition; however, we could be sure subjects had no significant eye movements because (i) several eye movements during the adaptation phase alter the location of adapting stimulus repeatedly in the retinotopic visual areas and could potentially attenuate the adaptation effect. However, we found a robust adaptation in this condition and (ii) upward fixation drifts could make the test illusory line highly visible and consequently minimize the difference between percentage correct of different adapt-test and same adapt-test; however, we observed a large difference between the two percentage corrects in this condition.

In poor attention condition, a dual task was performed at the fixation point. At the end of adaptation phase, subjects were instructed to shift their attention toward the location of test stimulus and report the orientation of the test illusory line, which was presented for only 580 msec. Because there was no delay between adaptation and test phases, subjects might not have enough time for task switching and attentional shift. This could potentially explain no adaptation effect in poor attention condition (i.e., equal percentage correct for different adapt-test and same adapt-test). Further analysis showed that the three attentional conditions had similar overall performance, which could rule out the abovementioned explanation for our results. High overall performance in poor attention condition confirmed that removal of digit stimuli in the last 500 msec of the adaptation phase was effective in disengagement of attention from the fixation point.

The illusory line-TAE is also modulated with object-based attention even if attended stimuli are less visually salient than non-attended ones. This fact shows strong modulatory effects of object-based attention on TAE to illusory lines. This result is also consistent with the idea that attention modulates adaptation of high-level cells whose responses saturate at low contrast (Cheng, Hasegawa, Saleem, & Tanaka, 1994).

In same tilt stimuli, both illusory lines in the transparent stimulus are tilted clockwise or counterclockwise, one from vertical and the other from horizontal. In these stimuli, direct TAE from one illusory line (e.g., the illusory line tilted clockwise from vertical) and indirect TAE from the other illusory line (e.g., the illusory line tilted clockwise from horizontal) are in different directions and may cancel each other. In attended condition, direct TAE for same tilt stimuli is considerably robust implying that attention could enhance direct TAE. In this case, attention-dependent direct TAE is stronger than indirect TAE from non-attended illusory line. On the other hand, TAE has been completely removed for same tilt stimuli in non-attended condition, which implies that indirect TAE from attended illusory line is enhanced and direct TAE from non-attended illusory line is attenuated; and, therefore, they would have approximately the same magnitude and could cancel each other (note that the perception of indirect TAE is generally weaker than that of direct TAE in classic versions of TAE (Campbell & Maffei, 1971)). Thus, we could conclude that both direct and indirect illusory line-TAEs are modulated and enhanced by attention (see Figure 10 for schematic explanation).

Classically V2 area is considered as the first stage in the processing of illusory contours (Peterhans & von der Heydt, 1982; von der Heydt, Peterhans, & Baumgartner, 1984). However, there are some data suggesting that illusory contours could be coded by cells in V1 (Grosof, Shapley, & Hawken, 1993; Sheth, Sharma, Rao, & Sur, 1996). Using an animated adaptation paradigm in Experiment 1, we minimized the adaptation to real lines. Also, the TAE to illusory lines in Experiment 2 cannot be explained by adaptation to the real lines. Therefore, we excluded the possibility of adaptation to illusory lines in lower visual areas than V1. We could conclude that selective visual attention modulates the activation of neurons in

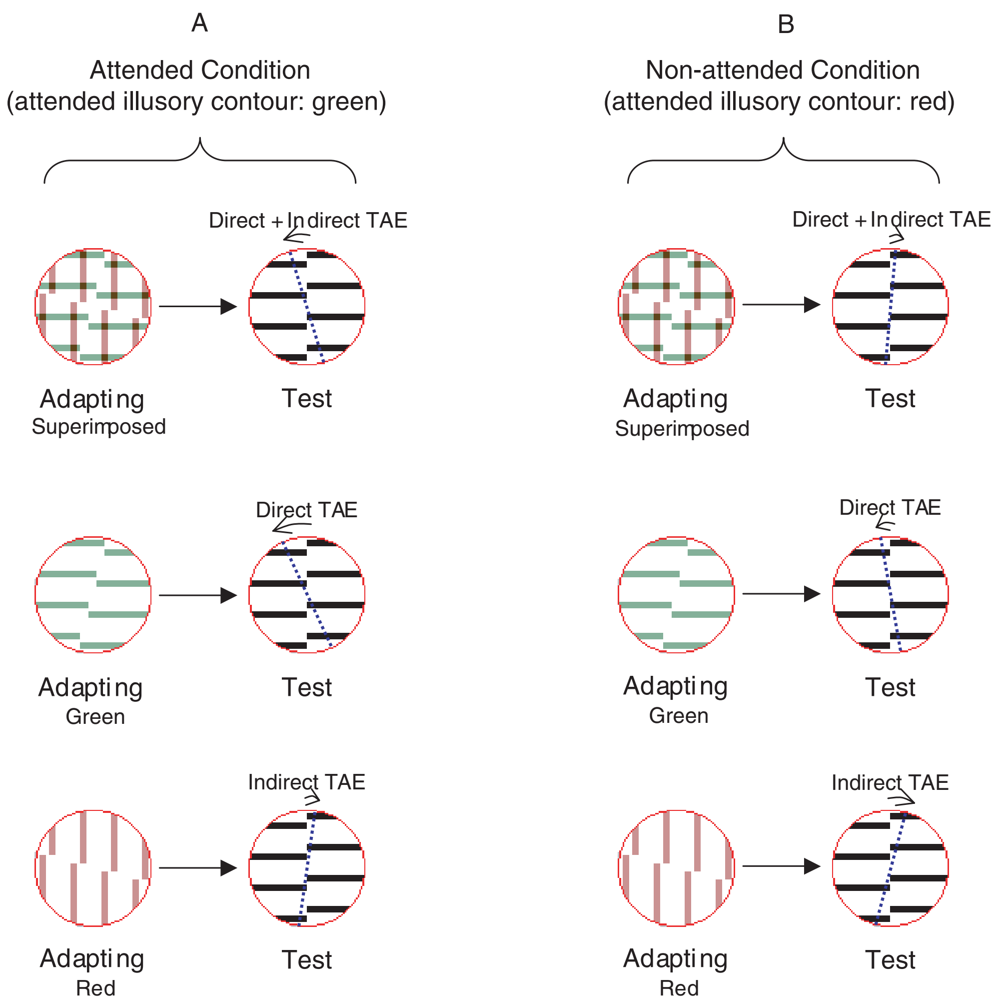

Figure 10. Theoretical explanation of how attention modulates and enhances both direct and indirect TAEs induced by illusory contours. If illusory contours are superimposed in the adaptation phase, perceived direction of tilt in the test phase will be determined by the interaction between direct TAE from one illusory contour and indirect TAE from the other (see text). Only same tilt stimuli have been shown in this figure. A. In the attended condition (attended illusory contour: green; test illusory line: vertical), a robust TAE was demonstrated (top row). This could be attributed to the superposition of a strong direct TAE from attended illusory line (middle row) with a weak indirect TAE from non-attended illusory line (bottom row). B. In the non-attended condition (attended illusory contour: red; test illusory line: vertical), almost no TAE was detected (top row). This could be explained by the superposition of an attenuated direct TAE from non-attended illusory line (middle row) with an enhanced indirect TAE from attended illusory line (bottom row).

early visual areas, presumably in V2 and V1 areas. Several electrophysiological studies have shown strong modulatory effects of attention on responses of V1 neurons (Ito & Gilbert, 1999; Motter, 1993; Roelfsema, Lamme, & Spekreijse, 1998) and V2 neurons (Bender & Youakim, 2001; Luck, Chelazzi, Hillyard, & Desimone, 1997; Motter, 1993; Reynolds, Chelazzi, & Desimone, 1999). Our results confirm this notion and provide psychophysical evidence regarding attentional modulation of adaptation to illusory lines, which most probably occurs in V2 and V1 areas.

Different hypotheses have been suggested to explain the neuronal mechanisms underlying the perception of illusory contours (Halpern, 1981). According to feature analyzers hypothesis, illusory contours result from the partial triggering of contour-specific neural units by the physically present edge along the inducing areas (Stadler & Dieker, 1972). Neural network models developed on the basis of this theory have successfully generated continuous contours (filling-in contours) from discontinuous stimulus (Grossberg & Mingolla, 1985). If we suppose that neurons or neuronal populations at inducing areas respond to illusory lines presented at their preferred orientation, the adaptation to illusory lines could be due to repeated firing of these neurons when the stimulus (illusory contour) is presented for a long exposure time (e.g., 4 s in Experiment 1, and 30 s in Experiment 2). Continuous neural firing decreases the orientation sensitivity maximally at the adapting orientation. According to the rate-based mechanism for attentional modulation, selective visual attention raises the firing rate of neurons at the attended location (Treue, 2001). Continuous firing of neurons at higher rates increases the susceptibility to neuronal adaptation and therefore leads to stronger adaptation to illusory lines. This mechanism could be a possible explanation for attention-dependent adaptation to illusory lines.

Conclusions

The present work shows that adaptation to illusory lines is weakened in the conditions of inattention (either when spatial or object-based attention is drawn away from adapting stimuli). In the previous study, we have shown that adaptation to illusory lines does occur without explicit conscious access to the orientation of illusory lines (Rajimehr, Montaser-Kouhsari, & Afraz, 2003). The unconscious condition was met by presenting the illusory contour in a severe crowding condition. Although performance of subjects in reporting the orientation of crowded illusory lines was at chance level, yet orientation selective adaptation was preserved for crowded as well as non-crowded adapting targets. How could we interpret these two different facts? The crowding effect we observed may have been due largely to an inability of attention to resolve the closely spaced targets (He, Cavanagh, & Intriligator, 1997). He, Cavanagh, and Intriligator (1996) have studied orientation selective adaptation in the crowding condition to show that crowding is a high-level phenomenon, which occurs at the level of attentional selection, not at an early sensory level. Therefore, adaptation occurs expectedly in the crowding condition when adapting stimulus is processed in the sensory level (e.g., illusory lines, which are processed in V2 and V1 areas). On the other hand, the effects of attentional modulation have been shown in the sensory levels (e.g., Motter, 1993). Thus, adaptation in some sensory levels would be attention-dependent. We could suggest that although we are not able to individuate the crowded target by attention, yet attentional modulations and attention-dependent adaptation exist subliminally for crowded targets. The fact that orientation selective adaptation occurs in primary visual cortex (V1) without awareness (He et al., 1996) but tilt aftereffect in V1 is attenuated without attention (Spivey & Spirn, 2000) provides another evidence for our suggestion. Further investigations (e.g., measuring adaptation to a crowded target while a dual task is performed at the fixation point) can clarify the role of attentional modulations in the crowding conditions.

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