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·Original Article·

Contextual influence on the tilt after-effect in foveal and para-foveal vision

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ABSTRACT

A sensory stimulus can only be properly interpreted in light of the stimuli that surround it in space and time. The tilt illusion (TI) and tilt after-effect (TAE) provide good evidence that the perception of a target depends strongly on both its spatial and temporal context. In previous studies, the TI and TAE have typically been investigated separately, so little is known about their co-effects on visual perception and information processing mechanisms. Here, we considered the influence of the spatial context and the temporal effect together and asked how center-surround context affects the TAE in foveal and para-foveal vision. Our results showed that different center-surround spatial patterns significantly affected the TAE for both foveal and para-foveal vision. In the fovea, the TAE was mainly produced by central adaptive gratings. Cross-oriented surroundings significantly inhibited the TAE, and iso-oriented surroundings slightly facilitated it; surround inhibition was much stronger than surround facilitation. In the para-fovea, the TAE was mainly decided by the surrounding patches. Likewise, a cross-oriented central patch inhibited the TAE, and an iso-oriented one facilitated it, but there was no significant difference between inhibition and facilitation. Our findings demonstrated, at the perceptual level, that our visual system adopts different mechanisms to process consistent or inconsistent central-surround orientation information and that the unequal magnitude of surround inhibition and facilitation is vitally important for the visual system to improve the detectability or discriminability of novel or incongruent stimuli.

Keywords: tilt after-effect; contextual influence; spatio-temporal context; foveal vision; para-foveal vision

INTRODUCTION

It is well established that a sensory stimulus can only be interpreted properly in light of the stimuli that surround it in space and time[1]. That is, how we perceive an object depends strongly on both its spatial context (what surrounds a given object or feature) and its temporal context (what has been observed in the recent past). The most straightforward examples are the tilt illusion (TI) and the tilt after-effect (TAE). In the former, the perceived orientation of a test line or grating is altered by the presence of surrounding lines or gratings with a different orientation (spatial context); the surround context and the target are separate in space but overlap in time. In the latter, the perceived orientation changes after prolonged inspection of other oriented lines or gratings (temporal context); the context of adapting lines and the test lines overlap in space but not in time. These center-surround spatial interactions or before-after temporal effects have given rise to many remarkable results and theories. The TI and TAE have been widely documented with various stimulus attributes, such as spatial frequency, color, luminance, and contrast differences between the test lines or gratings and the contextual ones[2-4]. Many experiments have indicated remarkable similarities between spatial and temporal contextual effects, although there are still some controversial results and explanations[1]. In neurophysiology, the TI is believed to be based on the known center-surround properties of neurons in early cortical areas and perhaps higher-level involvement[5], while for the TAE, it is usually supposed that adaptation leads to the suppression of neuronal responses near the adapting orientation[6,7]. However, the recent study by Wissig and Kohn showed that adaptation not only causes stimulus-specific suppression of responsivity and repulsive shifts in tuning preference, but also leads to response facilitation and shifts in tuning toward the adapter[8].

Although spatial and temporal effects always co-exist in natural visual scenes, only a few behavioral studies have investigated the spatio-temporal effects on orientation perception. Guo *et al.* explored how manipulating the spatio-temporal prior probability of stimuli affects human orientation perception, and found that a predictable spatio-temporal stimulus structure and an increased probability of collinear trials are associated with an increasing prior expectation of collinear events[9]. Durant *et al.* investigated the spatio-temporal interaction of the TI by presenting components of the stimulus asynchronously, and found that in conditions when the only feature difference between surround and center is orientation, the TI is greatest when the center and surround are presented simultaneously. But introduction of an additional segregation cue such as a spatial gap, differential contrast, or relative depth reduces the size of the TI when the two parts of the stimulus are presented simultaneously[10]. However, few studies have investigated the effect of the interaction between center and surround stimuli on the TAE, especially comparing the magnitudes of inhibition and facilitation for both the fovea and para-fovea. Actually, Xing *et al.* examined center-surround interactions in foveal and peripheral vision using contrast-matching tasks and found that surround suppression became markedly stronger as the center-surround stimulus was moved toward the periphery and surround facilitation diminished in the periphery. These results imply that center-surround interactions play different functional roles in the fovea and periphery[11]. In previous TAE studies, adapting gratings were typically large areas of congruent patches that spatially overlapped with the test patches[4,12]. Little is known about how an incongruous center-surround patch affects our subsequent perception of a target. Little is known about the resulting TAE if the adapting patches do not spatially overlap but surround or are adjacent to the test patches. Most importantly, little is known about the functional benefit of surround inhibition or facilitation in foveal and para-foveal perception. In fact, in the real world, complex or nearby contextual effects are common. Studying the effect of center-surround interaction on the TAE would help reveal the underlying neuronal mechanisms involved in visual processing and how they interact with each other in spatio-temporal dimensions.

In this study, four types of center-surround adaptation patterns were used to examine the influence of spatial context on the TAE. Test stimuli were presented in the fovea and the periphery, and the magnitudes of surround or center inhibition and facilitation were compared to explore how center-surround interaction affects the TAE in foveal and para-foveal vision.

METHODS

Participants

Eight right-handed participants (three male and five female) aged 23–29 years (average age 24.8) volunteered for this study. All participants had normal or corrected-to-normal vision and provided written informed consent prior to participation. The experimental paradigms were approved by the Ethics and Human Participants in Research Committee at the University of Electronic Sciences and Technology of China in Chengdu, China. All participants volunteered for the experiments and did not know anything about their purpose (except for one of the authors). Orientation perception of the test stimuli presented in foveal and para-foveal vision was tested before the formal experiment. The participant did not have prior exposure to any of the adapting stimuli. One participant who had a large inherent bias to orientation discrimination was excluded. The other seven were given 30 min of initial training before the experiments to become familiar with the task. Data from the training session were not included in the final analysis.

Each participant performed 8 sessions for the foveal and para-foveal conditions. Each session included 7 blocks, and each block included 28 trials, resulting in a total of 1568 individual trials.

Experimental Setup

The tasks were performed in a dim and sound-attenuated room designed for psychophysics experiments, and illumination was held constant for all participants. The participants viewed the display from a distance of 57 cm, and their head movements were restricted by forehead and chin rests. The stimuli appeared on the center of a grey background, which was adjusted to a mean luminance of ~22 cd/m^2. The stimulus-presentation program was compiled in MATLAB (MathWorks, Natick, MA) using Psychtoolbox[13,14]. The stimuli were presented on a display computer with a high-resolution color monitor (1024×1280 pixels, 3×8 bit RGB) and a 100-Hz refresh rate.

Previous studies have shown that the TAE might produce spatiotopic transfer across or after saccades[15,16]. The results would be biased if participants moved their eyes frequently during the experiments. Therefore, although all participants were trained psychophysical observers and could maintain proper fixation, we nevertheless monitored their eye movements to ascertain that they did not move their eyes during the experiment. Eye movements were recorded with an infrared eye tracker (Eyelink2000, SR Research Ltd.) and sampled at 1 000 Hz. The pupil of the left eye was tracked at a sample rate of 1 000 Hz.

Stimuli

The adapting stimuli (adaptors) were composed of two parts: center and concentric annular surround patches, which were sinusoidal gratings tilted 20° clockwise or counterclockwise from the vertical. The radius of the central grating was 1°, and that of the surround was 5°. The contrast was 0.9. There were four patterns of adaptors (Fig. 1B): (A) a center-only grating patch; (B) a surround-only grating patch; (C) cross-oriented center and surround grating patches; and (D) iso-oriented center and surround grating patches. All the patches in the four patterns randomly tilted clockwise or counterclockwise.

The test grating was 1° in radius and the contrast was 0.7 to induce a large TAE[17]. The orientation of the test grating was one of the following: −4°, −2°, −1°, 0°, 1°, 2°, or 4° (0° refers to the vertical, negative and positive orientations indicate leftward and rightward tilts, respectively) when presented in the center and one of the following: −6°, −4°, −2°, 0°, 2°, 4°, or 6° when presented on the left or the right 3° away from the center, which was in the para-foveal region of the visual field. When the test was presented in the periphery, the visual acuity of physical orientation dropped, and a large physical tilt was required to compensate for the strong after-effect[18].

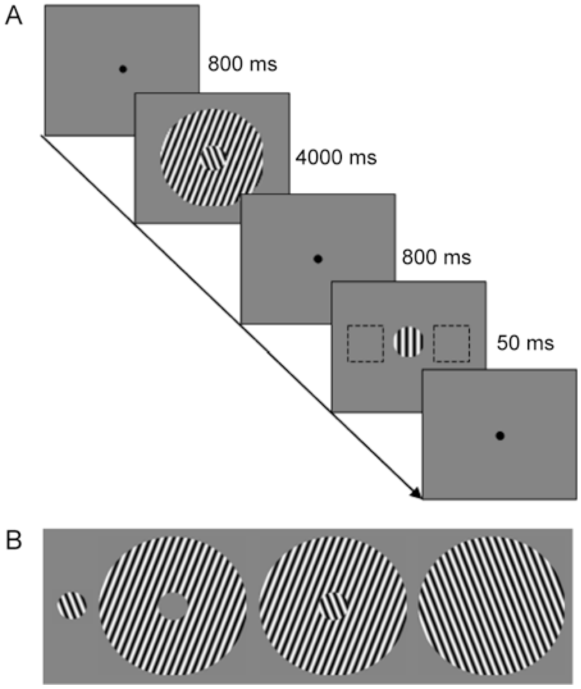

Fig. 1. The experimental paradigm (A) and the four adaptor patterns (B). From left to right, the adaptors were center-only, surround-only, cross-oriented center and surround, and iso-oriented center and surround grating patches.

Procedure

Each trial started with the appearance of a black fixation dot (0.2º in diameter) at the center of the screen for 800 ms, followed by the appearance of an adaptor for 4 000 ms (Fig. 1). In the center of the adaptation stimulus was a very light-gray point (0.2º in diameter) to help observers fixate at the center. Then a blank grey screen with a fixation point appeared. After an 800-ms delay, a test grating was presented for 50 ms in the center or the periphery of the screen. When the test grating was randomly presented either on the left or on the right, there was a fixation point in the center. The participants were asked to fixate on the fixation point and to blink as little as possible during the trial. After test stimulus presentation, observers responded using the arrow keys on the keyboard, indicating the perceived orientation of the test stimulus (tilted to the left or to the right), and then pressed any key to start the next trial.

Data Processing and Analysis

The method of measuring TAE magnitude was similar to that described by David Melcher[19]. The responses of each participant were normalized by his/her perception of a target without prior exposure to any adapting stimuli to eliminate internal bias. The proportion of trials in which the observer responded "Left" was calculated for each test stimulus orientation for each condition. The data from each participant were fit with a sigmoid Boltzmann function[20]. The midpoint of this function was used as the estimate of the point of subject equality, at which participants perceived the stimulus as tilted to the left in 50% of the trials. Adaptors tilted leftward and rightward were plotted separately to measure the distance between the two psychophysical curves. The distance between the 50% point for leftward- and rightward-tilted adaptors was calculated as the magnitude of the TAE. In our study, "Left" of the center grating was regarded as the reference orientation when calculating the TAE.

One-way analysis of variance (ANOVA) with least significant difference was used for TAE comparisons among adapting patterns in each foveal and para-foveal condition.

To ensure that the TAE under fixation conditions was not contaminated by saccades, eye-movements were monitored during the experiment. If saccades occurred or the gaze position deviated >1° from the fixation point during one trial, that trial was discarded and another trial was automatically added. An example of the real fixation positions and their distribution in one block under one adapting condition is illustrated in Fig. 2. In this way, we ensured that the eyes were always fixated at the fixation point no matter what test stimulus was presented in the foveal or para-foveal position under the four adapting conditions. In total, <1% of trials were automatically added.

RESULTS

Effect of Center-Surround Interaction on TAE in Foveal Vision

The TAEs of the four adapting patterns for each of the seven participants when test gratings were presented in the center are shown in Fig. 3. The distance (in degrees of orientation) between the two curves was calculated as the magnitude of the TAE for each adapting pattern when the observer responded "leftward" in 50% of the trials[19]. The greater the distance between the two curves, the larger the tilt aftereffect. The individual and mean magnitudes of the

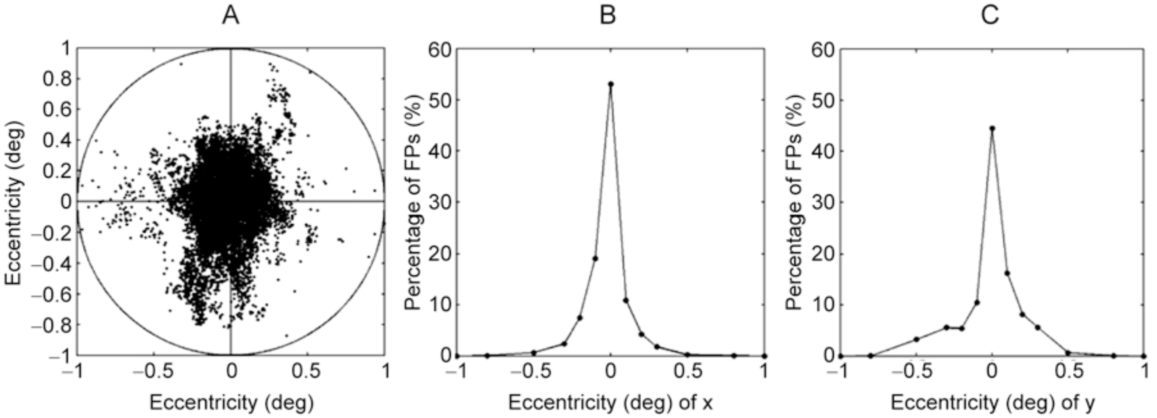

Fig. 2. **An example of real fixation positions (FPs) and their distribution in one block under one adapting condition. (A) Distribution of real FPs during the task in one block. The circle surrounding the points indicates a range of 1º of visual angle. (B and C) Curves of the relative number (%) of real FPs over the horizontal and vertical axes; both show a normal distribution with a peak at the assigned fixation point (0º eccentricity).**

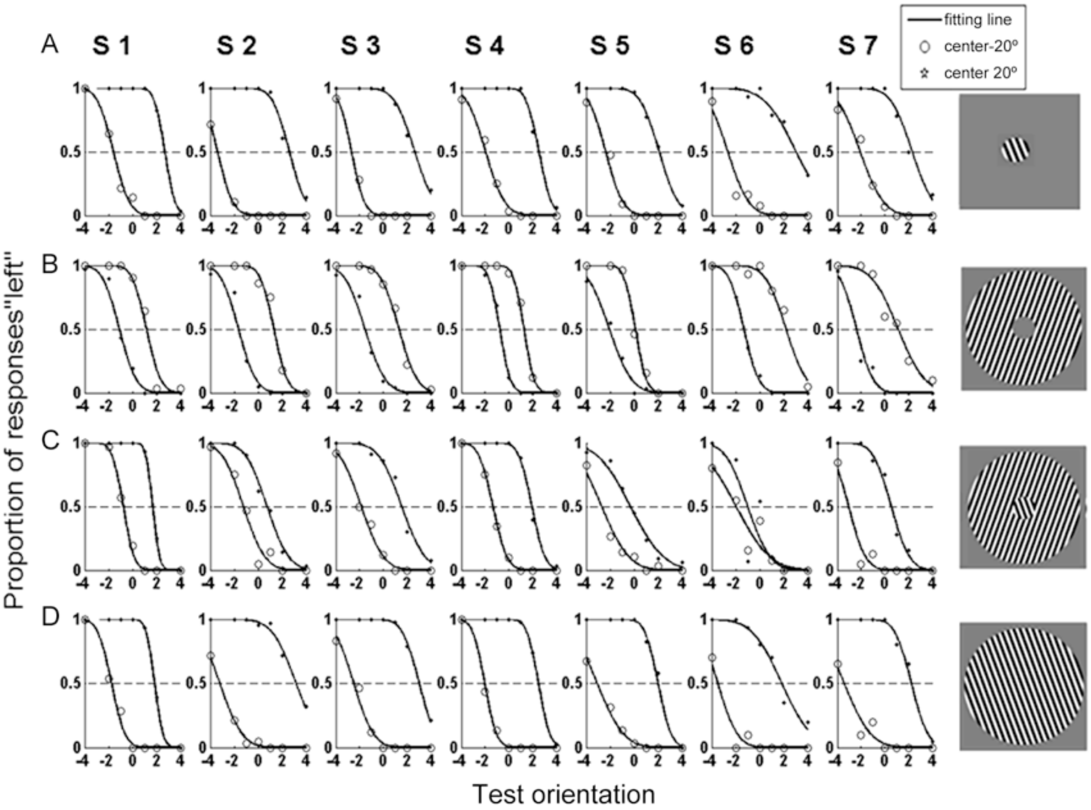

Fig. 3. Tilt after-effects for the four adapting patterns (A-D; right panel shows the corresponding adaptor patterns) for each of the seven participants (S1–S7) when test gratings were presented in the fovea. The proportion of trials in which the test stimulus was perceived as tilted leftward is plotted as a function of test stimulus orientation. The two curves show average performance for the adaptors oriented +20º and −20º from the central orientation. The distance (in degrees of orientation) between the two curves was calculated as the magnitude of the tilt after-effect for each observer in each condition when the observer responded "leftward" in 50% of the trials (horizontal dashed line).

TAEs induced by the four adaptor patterns in foveal vision are shown in Fig. 4. As the orientation of the surround was the opposite of the reference "Left" in the surround-only adapting condition, the TAE value in this condition was negative. One-way ANOVA showed a marked difference in TAE magnitude among the four adapting patterns (F = 112.88, P <0.001). A strong TAE occurred in the fovea in the presence of the central grating only, where the test overlapped with the adaptor in space (Fig. 4, pattern A). Interestingly, an inhibiting TAE was also induced with only a large surrounding grating patch, although the test did not spatially overlap with the adaptor in this condition. However, the magnitude was much smaller than that induced by the center patch only (P <0.001). Nevertheless, we can still say that in this condition, the perceived orientation was influenced by the surround grating; i.e., a vertical line looks slightly tilted in the direction opposite to the orientation of the surround grating (pattern B). When the adaptor consisted of cross-oriented center-surround patches, the TAE magnitude decreased markedly compared with the central grating only condition (P <0.001), which implied that a surround grating with inconsistent orientation significantly inhibited the TAE (comparison of patterns A and C). However, when the central and surround gratings had consistent orientation, the TAE magnitude increased slightly compared with the central grating only condition, but there was no difference (P = 0.68) (comparison of patterns A and D). Similarly, the TAE magnitude in the iso-oriented adaptor condition was stronger than that in the surround-only (P <0.001) and cross-oriented (P <0.001) conditions

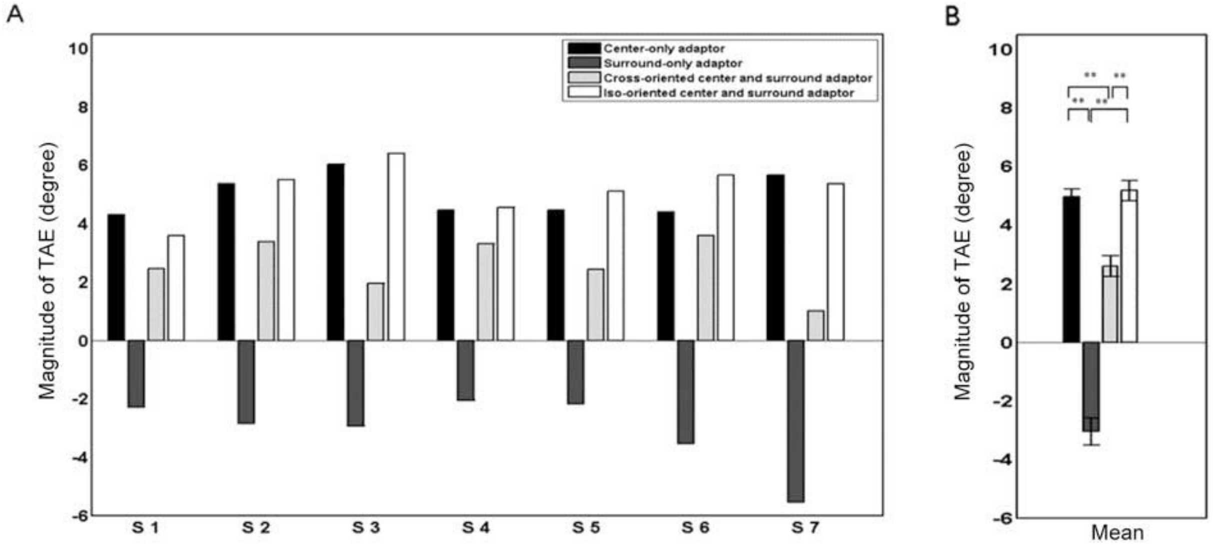

Fig. 4. The individual (A) and mean magnitudes (B) of the tilt after-effect in foveal vision for seven participants. The vertical lines represent the SD. ***P* <0.001.

(comparison of patterns D, B, and C).

From data such as that shown in Fig. 4A, we calculated the magnitude of the TAE of surround inhibition in foveal vision from the TAE of cross-oriented center-surround patches by subtracting that of the center-only patch. Similarly, the TAE of surround facilitation in foveal vision was calculated from the TAE of the iso-oriented center-surround patches by subtracting that of the center-only patch. The average TAEs of surround inhibition and facilitation for the seven participants are shown in Fig. 5. A negative TAE value indicates that the cross-oriented surround patches inhibited the TAE of the central patches while a positive value indicates that the iso-oriented surround patches facilitated the TAE of the central patches. There was a marked difference between surround inhibition and facilitation (*P* <0.001), and the cross-oriented inhibition of the surround grating was much greater than the iso-oriented facilitation in foveal vision.

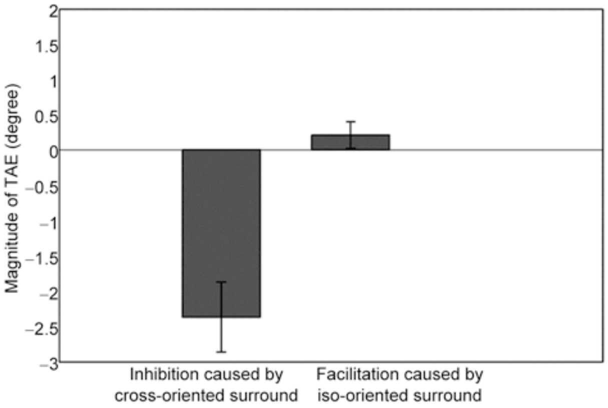

Fig. 5. The tilt after-effect of inhibition caused by cross-oriented surround and facilitation caused by iso-oriented surround to the central test in foveal vision. The vertical lines represent the SD.

Effect of Center-Surround Interaction on TAE in Para-foveal Vision

Similarly, the TAEs for the four adapting patterns for each of the seven participants when test gratings were presented in the para-fovea are shown in Fig. 6. The individual and mean magnitudes of the TAE induced by the four types of adaptors in para-foveal vision are illustrated in Fig. 7. As the participants were instructed to gaze at the central fixation point, and the test did not spatially overlap with the central adaptor, when the adaptor was a center-only grating, the TAE was smallest, indicating that the center grating had a very weak aftereffect on the subsequent surround test (Fig. 6, pattern A). However, since the test stimuli overlapped with the surrounding adapting gratings in space, the surround-only grating patch produced a strong TAE, which was markedly greater than that of the center-only grating

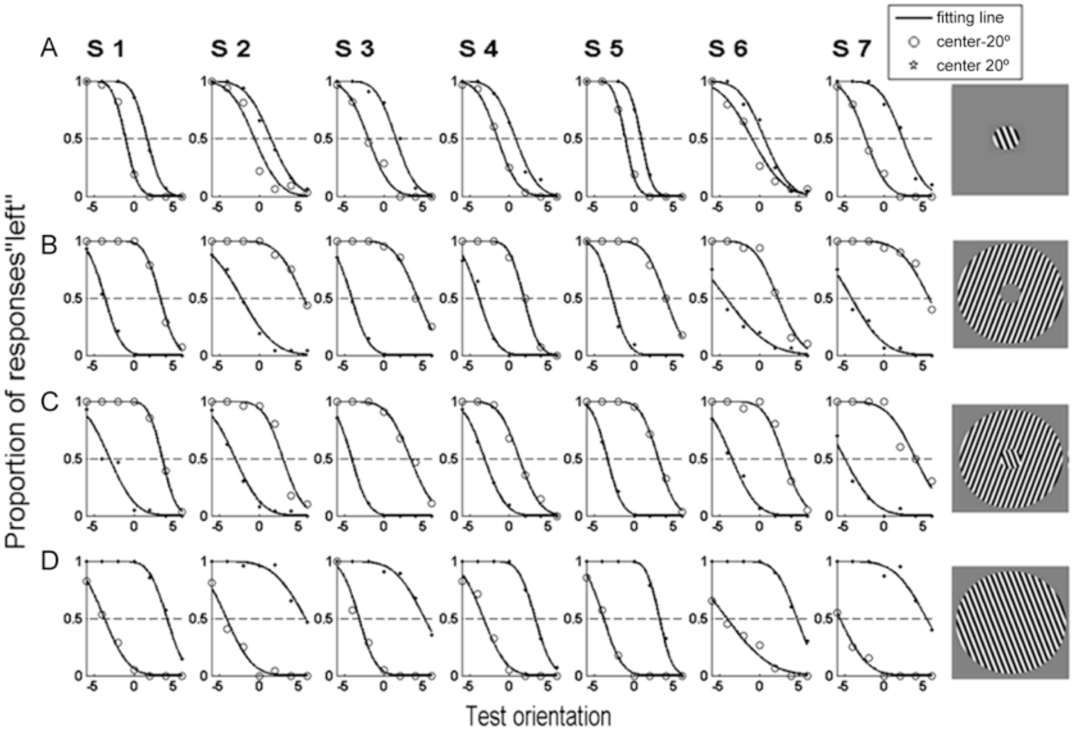

Fig. 6. Tilt after-effects for the four adapting patterns (A-D; right panel shows the corresponding adaptor pattern) for each of the seven participants (S1–S7) when test gratings were presented in the para-fovea.

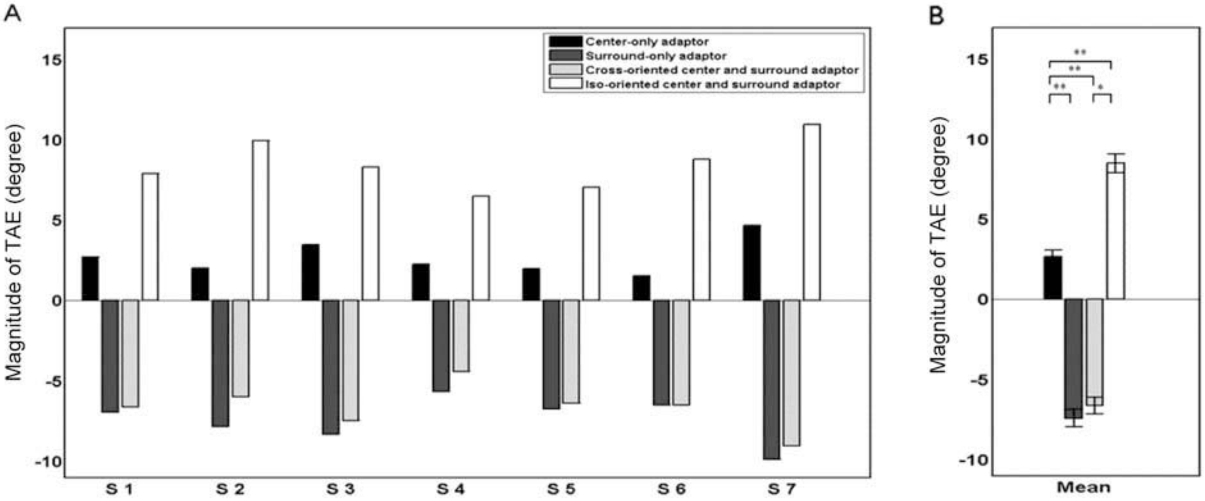

Fig. 7. Individual (A) and mean magnitudes (B) of TAE in para-foveal vision for seven participants. The vertical lines represent the SD. $^{*}P$ <0.05. $^{**}P$ <0.001.

(*P* <0.001, comparison of patterns B and A). In the cross-oriented condition, the TAE was also negative, implying that it was mainly induced by the large surrounding patches in para-foveal vision. The TAE magnitude in the cross-oriented condition was also stronger than that of the center-only adapting condition (*P* <0.001) but was slightly weaker than that of the surround-only condition, implying that the cross-orientated central gratings give rise to suppression of the surround, but the influence was not significant (*P* = 0.297, comparison of patterns C and A, B). The TAE in the iso-oriented condition was the strongest, because the central patch facilitated the surround when they had same orientation (pattern D). Statistical analysis showed that there was no difference between the TAE of the iso-oriented condition and that of the surround-only condition (*P* = 0.153, comparison of patterns B and D), but a difference existed between the TAE of the iso-oriented and the cross-oriented conditions (*P* = 0.018, comparison of patterns D and C). One-way ANOVA also showed a difference in the TAE among the four adapting patterns in para-foveal vision (*F* = 23.727, *P* <0.001).

Similarly, from data such as that shown in Fig. 7A, we calculated the magnitude of the TAE of central inhibition by taking the magnitude of the TAE of the cross-oriented center-surround patches and subtracting that of the surround-only patch. Likewise, the TAE of center facilitation was computed by taking the magnitude of the TAE of iso-oriented center-surround patches and subtracting that of the surround-only patch. The average TAE magnitudes of center inhibition and facilitation for the seven participants are shown in Fig. 8. There was no difference between the magnitude of center inhibition and facilitation (*P* = 0.352), showing that even though the center-surround interaction also significantly affected the TAE of para-foveal vision, center inhibition and facilitation in the surround test were less sensitive in para-foveal vision than the surround inhibition and facilitation in foveal vision.

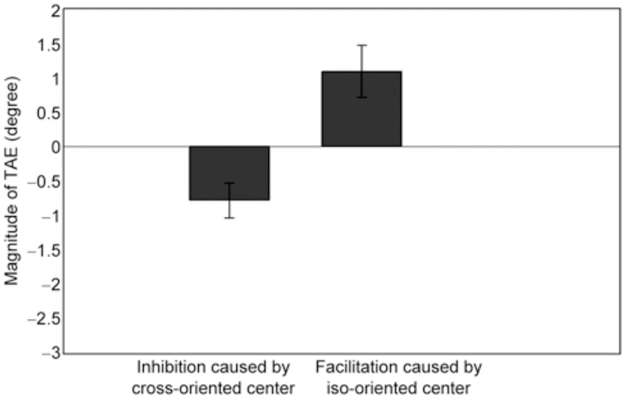

Fig. 8. TAE of inhibition caused by cross-oriented center and facilitation caused by iso-oriented center in para-foveal vision. The vertical lines represent the SD.

DISCUSSION

In this study, we investigated the influence of center-surround spatial interactions on the perception of a stimulus viewed subsequently in foveal and para-foveal vision, taking the spatial contextual influence and temporal effect into consideration together. Our main finding was that consistent or inconsistent center-surround spatial interaction significantly affected the TAE of both foveal and para-foveal vision. In the fovea, the TAE was mainly produced by central adapting gratings. A cross-oriented center-surround grating significantly inhibited the TAE, and an iso-oriented one slightly facilitated it. However, the inhibition was much stronger than the facilitation. In the para-fovea, the TAE was mainly determined by the surrounding patches. Likewise, a cross-oriented center-surround grating inhibited the TAE, and an iso-oriented one facilitated it. However, there was no significant difference between inhibition and facilitation.

Muir *et al.* studied the TAE in central and peripheral vision in the early 1970s, and their results showed a strong TAE when the adaptor and test contours coincided spatially. However, inspection of a tilted line in half of the visual field had no influence on subsequent judgments of the orientation of a line displayed in the opposite half[21]. Our results are consistent with their findings to some extent; specifically, the TAE was highly specific for a limited spatial location. A strong TAE occurred when the test spatially overlapped with the adaptor, regardless of whether the target was presented in foveal or para-foveal vision. However, we found that a slight TAE was also produced if the test did not spatially overlap with the adaptor. Our results showed that the surround-only adaptor also induced a comparative TAE in the blank center. This is consistent with the findings of Greenwood *et al.*, who showed that a TAE occurs in a blank space when a vacant center is crowded by four iso-oriented flankers, which is known as the crowding phenomenon[22].

Recent electrophysiological studies have proposed that adaptation leads to the suppression of neuronal responses near the adapting orientation, and this is typically understood to be an automatic process in the primary visual cortex[8,23]. The stronger the suppression, the larger the TAE. We know that many neurons in the primary visual cortex are selective for local orientation within spatial receptive fields. An inhibitory or facilitatory non-classical, extra-receptive field (ERF) exists outside of the classical receptive field for most neurons in the primary visual cortex[24]. Contextual stimuli with different texture features (orientation, spatial frequency, and speed and direction of movement) can activate cells with inhibitory ERFs, whereas those with similar features can excite neurons with facilitatory ERFs[25]. Li *et al.* proposed that the inhibitory ERF may function as a heterogeneity-detector and that the facilitatory ERF may function as a homogeneity-detector[26]. Our results showed that the TAE was strongest when center and surround patches were iso-oriented, no matter what test was presented in the fovea or para-fovea, because similar center-surround features facilitate the suppression of neuronal responses. The TAE was reduced when center and surround patches were cross-oriented because different center-surround features weaken the suppression of neuronal responses. Our results seem to agree with the neuronal mechanism of the TAE on the perceptual level. Moreover, our results demonstrated that the magnitudes of surround inhibition and facilitation differed in foveal vision. The cross-oriented inhibition of the surround grating was much larger than the iso-oriented facilitation in foveal vision, providing powerful evidence that our visual system is a highly non-linear processing system during orientation perception, implying that it may use different mechanisms to deal with consistent or inconsistent orientation information. The importance of the unequal magnitudes of surround inhibition and facilitation may lie in improving the detectability or discriminability of novel or incongruent stimuli. In this way, the visual system could become more sensitive and effectively detect subtle surround variations within common stimuli.

Our results also showed that inhibition and facilitation of the central grating to a subsequent surround test were less sensitive in para-foveal than in foveal vision. Solomon and others have proposed that foveal and para-foveal processing are qualitatively different[18] and our results are consistent with this. We found that the absolute magnitudes of the TAE in the periphery (Fig. 7) were markedly larger than those in the center (Fig. 4) for the four adapting patterns, indicating that peripheral vision contains less precise spatial orientation information than foveal vision[21]. Note that, our visual system is a nonlinear information processing system to cope with various nonlinear interactions. The inhibition and facilitation of center-surround interactions in this study were only calculated and compared by simple algebraic summation from the four adaptors. Further experiments are anticipated to set up a fitted model to estimate the psychometric parameters for better understanding the nonlinear center-surround interactions in orientation perception.

In summary, we studied the effect of center-surround interaction on the TAE, and our results indicated that consistent or inconsistent center-surround spatial interaction significantly affected the TAE of both foveal and para-foveal vision. Similar center-surround features facilitated the TAE, while different features inhibited it. Our results also showed that the inhibition of the surround grating was significantly greater than the facilitation in foveal vision, although the inhibition and facilitation of the central grating to a subsequent surround test were less sensitive in para-foveal vision. Our results demonstrate on a perceptual level that our visual system uses different mechanisms to process consistent and inconsistent center-surround orientation information. As David Heeger noted, center-surround interactions in the fovea and periphery are incommensurable and play different functional roles in human image processing[11].

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