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Short communication

Static motion aftereffect does not modulate positional representations in early visual areas

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Abstract

A stationary stimulus is perceived to drift in the opposite direction after adaptation to a moving stimulus (static motion aftereffect (MAE)). It is commonly assumed that positional effects from the static motion aftereffect are mediated by early visual areas. Here we psychophysically showed that these positional effects did not modulate illusory line-tilt aftereffect (TAE). Since illusory contours seem to be represented at relatively early stages of visual hierarchy, we suggest that the neural substrates underlying the perception of static motion aftereffect and illusory contours are different.

Theme: Sensory systems
Topic: Visual psychophysics and behavior

Keywords: Static motion aftereffect; Tilt aftereffect; Illusory line; Visual hierarchy

The motion aftereffect (MAE) is a visual illusion, which refers to the modification of motion perception following prolonged observation of a regularly moving stimulus. This illusion is considered to be the perceptual manifestation of motion sensors recovering from adaptation. Typically MAE involves the apparent motion of a stationary stimulus in the opposite direction to a moving one observed previously (static MAE) [6,18]. It has recently been shown that the perceived position of objects can be markedly influenced by motion adaptation. In other words, MAE is accompanied by a shift in perceived spatial position of the pattern being viewed [7,9].

Psychophysical evidence, including partial interocular transfer of the static MAE, suggests that the effect is mediated in part by the striate cortex (V1) [8,18]. Neuroimaging studies in human have revealed that motion area MT+ shows enhanced activity during the perception of MAE when static test stimuli are used. The correlation between neuronal activation and perception of static MAE is stronger in MT+ than the low-level cortical areas such as V1 and V2 [1,4,16].

Thus, there are substantial controversies about the level of visual processing at which static MAE is encoded. Here, we decided to compare the processing level of static MAE to that of another previously known illusion whose level of processing had been fairly well determined and we chose illusory line-tilt aftereffect for this comparison. Following prolonged viewing of an illusory line slightly tilted from horizontal, observers perceive a horizontal illusory line (in the same region of the visual field) as being tilted in the opposite direction. Such angular repulsion effect is named direct tilt aftereffect (TAE) in subjective contours [10]. Neurophysiological experiments have shown that illusory contours are represented at relatively early stages in the visual system such as area V2 [17] and V1 [3,14].

We designed an adaptation paradigm to investigate the interaction between static MAE and illusory line-TAE. In this paradigm, an illusory contour was physically induced by abutting gratings, but perceptually made invisible to the viewer by apparent position shifts due to static MAE. We

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addressed the question whether such illusory contour is capable of inducing (maintaining) the TAE.

The adaptation paradigm consisted of three phases: adaptation, 'selective perceptual alignment' (SPA) and test. As shown in Fig. 1, there were two conditions (i.e., main and control) in each trial of the experiment. A typical trial began with the presentation of a red spot at the fixation point followed by presenting a window on each side of the fixation point. In each window, two line-gratings abutting each other moved along the horizontal axis but in opposite directions. Motions of the line-gratings in different directions produced a motion-defined border with constant orientation (an illusory line tilted either 15° clockwise or counterclockwise from horizontal). Tilt direction of the illusory line was varied independently for the two windows. In one window (e.g., left window in Fig. 1), the motion directions of line-gratings were constant during the whole 30 s of adaptation period (adapting stimulus in the main condition). In the other one (e.g., right window in Fig. 1), the motion direction of each line-grating reversed to its opposite direction every 5 s (adapting stimulus in the control condition). The direction of moving abutting gratings in the main condition was chosen randomly in each trial. Using the above-mentioned procedure, MAE was elicited only in the main condition while adaptation to the illusory line was maintained in both conditions. After 30 s, static line-gratings were presented in both windows (SPA phase). Static line-gratings abutted each other with a slight phase shift on the main condition side (e.g., left side in Fig. 1); however, they could be 'perceptually' aligned due to shift of position induced by MAE (the phase offset producing the illusory contour in static abutting gratings was set in the direction opposite to that of gratings' motion; hence, the MAE could potentially cancel the offset and align the gratings). Static line-gratings appearing on the control condition side (e.g., right side in Fig. 1) had no phase offset and were therefore 'physically' aligned. At the beginning of SPA phase, marked by the cessation of motion in the two windows, subjects pressed a key and held it down when the two windows looked similar and released the key immediately upon detecting the illusory line in one window. The test phase began when the key was released and static line-gratings containing a horizontal illusory line (test stimuli) were presented in both windows. Subjects reported the perceived tilt of the illusory line (slightly tilted clockwise or counterclockwise from horizontal) for both windows using a two-alternative forced-choice (2-AFC) procedure. The order of judgments for the two windows was fixed (first for the right window and then for the left window) but the location of main or control condition was chosen randomly in each trial.

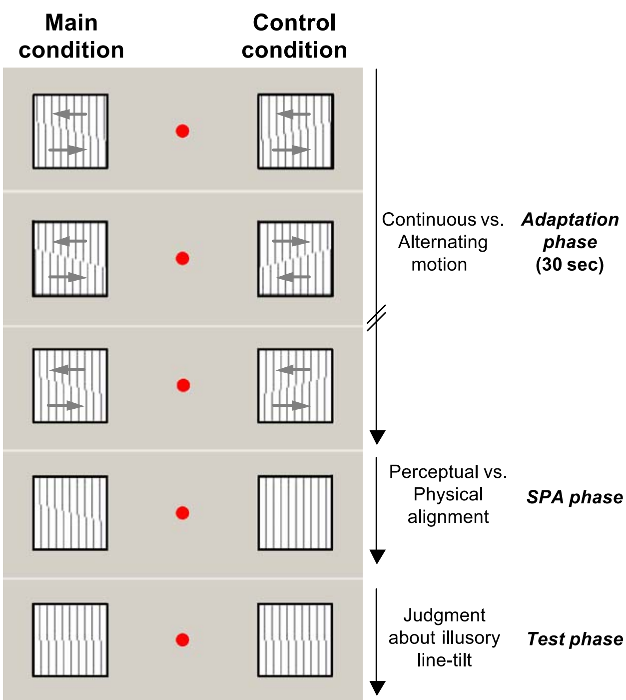

Fig. 1. Schematic diagram demonstrating the temporal succession of visual stimuli in a typical trial of the first experiment. In the adaptation phase two windows, each 4.57 × 4.57° in size, were presented in both left and right sides of the fixation point (eccentricity = 9.09°). In each window two line-gratings (the line width = 2.7 min) abutting each other, move with the speed of 0.91 deg/s in the horizontal orientation but different directions. The spatial frequency of each line-grating was 2.18 line/deg. The illusory line between two moving line-gratings was tilted either 15° clockwise or counterclockwise. During 30 s of adaptation period, the motion direction of line-gratings was constant in the main condition while it changed to its opposite direction every 5 s in the control condition. After 30 s, static line-gratings were presented in both windows (the phase of 'selective perceptual alignment'—SPA). Line-gratings abutted each other with $2\pi/5$ phase shift in the main condition ('perceptual alignment') and no phase shift in the control condition ('physical alignment'). Subjects pressed a key and held it down when both windows looked similar and released the key when the illusory line was perceived in one window. When the key was released, static line-gratings containing a horizontal illusory line with $2\pi/5$ phase shift were presented in both windows (test phase). Subjects reported the perceived tilt of illusory line (slightly tilted clockwise or counterclockwise from horizontal) for both windows. Three naïve subjects participated in the experiment and each subject completed five blocks consisting of 10 randomized trials. The distance between eyes and the screen was 50 cm.

In the minimal portion of trials, which we call 'catch trials', the offset in the SPA phase of the main condition was set in the same direction as the gratings' motion. It was expected that subjects did not experience any 'perceptual alignment' in the catch trials (as proved later in the analysis of catch trials). Subjects pressed another key when they had no perception of alignment and test stimuli were then presented immediately.

Results showed that illusory line-TAE was significantly attenuated in the control condition compared to the main condition ($P < 0.05$ in each subject separately, using two-tailed paired t-test) (Fig. 2a). Index of illusory line-TAE 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. This index was above 90% for the main condition in all subjects demonstrating a robust adaptation to illusory lines in the main condition.

The period of 'perceptual alignment' (induced by static MAE) in the main condition lasted longer than 1 s in all

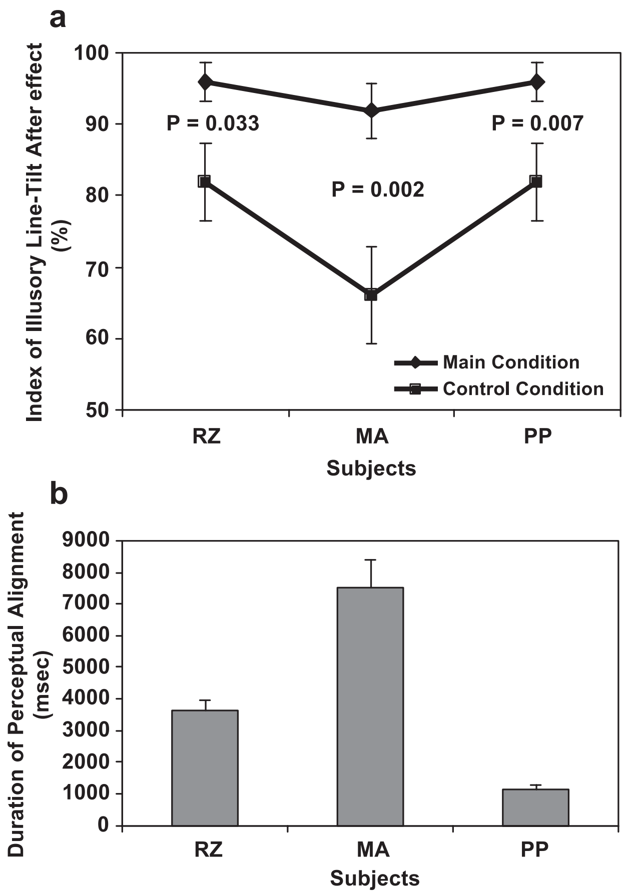

Fig. 2. (a) The index of illusory line-TAE in main and control conditions measured for each subject separately. This index was defined as the percentage of trials where the perceived tilt of the illusory line in the test stimuli was in opposite direction to the illusory line's tilt in the adaptation period. TAE was robust in the main condition while it was attenuated in the control condition. (b) Duration of 'perceptual alignment' period is shown for each subject separately. Error bars represent one standard error of mean.

subjects confirming the perceptual position shift during static MAE (Fig. 2b). In one subject who reported longer duration of 'perceptual alignment' in SPA phase, the illusory line-TAE was severely attenuated in the control condition (Fig. 2).

Expectedly there was no occurrence of 'perceptual alignment' in all catch trials. We added catch trials to make sure subjects were reliably reporting the 'perceptual alignment' and thus TAE was not analyzed in these trials.

Our experiment demonstrated a dissociation between the adaptation indices of the main and control conditions. In the main condition where abutting gratings were perceptually (but not physically) aligned, no recovery from tilt adaptation was observed. There was no adaptation effect for illusory line in the control condition during the SPA phase when physically aligned abutting gratings were presented and recovery from adaptation was observed in this condition. Reduced adaptation in the control condition could be attributed to the storage of adaptation during 30 s of adaptation period.

It may be claimed that the shearing motion itself, whether real or an aftereffect, might make the border defined by the shear (motion-defined border) rotate slightly. Further analysis showed that the perceived tilt in the main condition did not depend on the direction of motion (e.g., top to the right, bottom to the left) (P>0.05 using two-tailed t-test).

We chose the offset very close to the detection threshold of static abutting gratings so that slight positional change induced by the MAE could easily make the illusory contour invisible. Therefore, it is unlikely to have residual offset during MAE-induced positional shift. On the other hand, we might have had MAE-induced 'overshift in position' of gratings, which could result in developing a new offset in the opposite direction. However, we saw in a pilot experiment that two static MAE's in the opposite directions could not produce an offset (positional shift) in physically aligned abutting gratings (probably due to robust perceptual stability of aligned abutting gratings than misaligned ones); thus, the MAE-induced 'overshift in position' of gratings was ruled out.

As the MAE weakens over time, returns after storage, or alternatingly appears and disappears, difference in the magnitude of the TAE in the two conditions might have been induced by the illusory contour weakly visible during the SPA phase of the main condition (especially near the end). We performed a second experiment to show that the TAE could be induced even during the partial periods of SPA phase when the contour is perfectly invisible. The design of the second experiment was similar to that of the first but a new control condition replaced the previous one. During the SPA phase of the new control condition, physically misaligned abutting gratings (the same stimulus as used in the main condition) were presented. Illusory contour was occasionally invisible in the main condition as a result of MAE-induced positional shift but clearly visible in the control condition. Tilt direction of the illusory line was varied independently for the two windows. Subjects pressed a key and held it down until they could see the illusory contour in both windows and then released the key. When the key was released, test stimuli were presented in both windows. The aim of the experiment was to demonstrate robust TAEs in both conditions so we used a nulling paradigm for measuring illusory line-TAE in the two conditions because the method used in the first experiment may be inappropriate here due to the ceiling effect. The illusory line in the test stimuli was tilted $\pm 5°$ (step $1°$) from horizontal, selected randomly for either condition in each trial. Subjects reported the perceived tilt of illusory line (either tilted clockwise or counterclockwise from horizontal) for both windows using 2-AFC procedure. Like the previous experiment, the order of judgments for the two windows was fixed but the location of main or control condition was chosen randomly in each trial.

The average duration of SPA phase was 3.574 ± 1.182 s in the second experiment. The frequency of 'counterclockwise judgment' was calculated for each orientation of test illusory line. The psychometric function derived from calculated points was fitted with a logistic fitting function (Fig. 3). The threshold of subjective perception of horizontal orientation was set to the orientation of the test illusory line at which the proportion of 'counterclockwise judgment' in the fitted function was 50% (see Fig. 3). The thresholds indicating the magnitude of illusory line-TAE in the main condition were 4.899 (standard error of estimate (SE) = 0.608) and −2.816 (SE = 0.964) degrees when adapting illusory line was tilted 15° clockwise and 15° counterclockwise, respectively. In the control condition, the thresholds were 5.938 (SE = 0.593) and −2.875 (SE = 1.085) degrees. Difference between the two corresponding thresholds of main and control conditions was less than sum of standard error of estimates for the two thresholds. Hence, the thresholds in main and control conditions did not have significant difference with 95% confidence interval. Therefore, in both conditions, for the test illusory line to be perceived as horizontal, it needs to be slightly tilted clockwise after adapting to an illusory line tilted 15° clockwise and slightly counterclockwise after adapting to a counterclockwise illusory line.

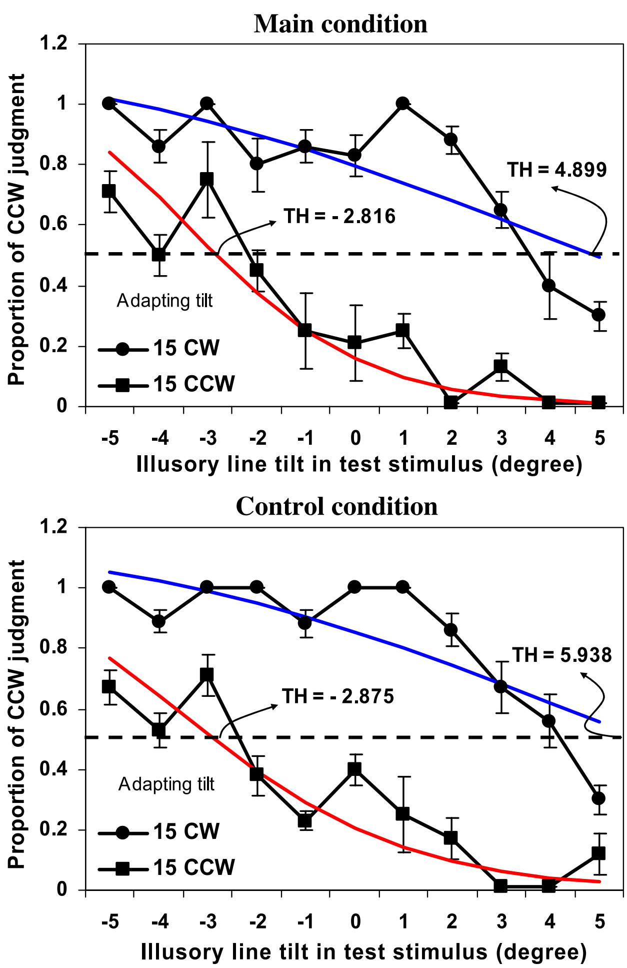

Fig. 3. Psychometric functions demonstrating the percentage of counterclockwise judgment for test illusory lines tilted ±5° (step 1°) from horizontal after adapting to a 15° clockwise and counterclockwise-tilted illusory lines in the main and control conditions of the second experiment. The threshold (TH) of subjective perception of horizontal orientation was set to the orientation of the test illusory line at which the proportion of 'counterclockwise (CCW) judgment' in the fitted logistic function was 50%. Data obtained from three naïve subjects were pooled to calculate the group average at each point because they showed very similar results. Each subject completed five blocks, each containing 50 trials. Error bars represent one standard error of mean.

The magnitude of TAE was equal in the main and control conditions implying that the TAE could be induced in the main condition even during the fraction of the SPA phase when the contour is perfectly invisible.

It has been estimated by single-unit recordings that ~20% of cells in V1 are directionally selective [2,13]; however, fMRI studies in humans and monkeys have revealed that the magnitude of direction selective adaptation in V1 is considerably smaller than that in V5 (MT) area and this magnitude gradually increases in hierarchical levels of motion processing [5,15]. Furthermore, cortical microstimulation of MT neurons can significantly bias perceptual judgments of motion direction, demonstrating a functional link between neural activity at the level of MT and motion direction judgments [12]. Previous studies suggest that the motion adaptation takes place at a relatively high level of motion analysis (probably at area V5/MT) and the representation of the position of spatial pattern in early stages of visual processing (such as areas V1 and V2, which represent local spatial information most precisely) is dynamically updated through feedback signals from neurons involved in the analysis of motion [7,9]. However, our results provide clear evidence against the conjecture that the motion signal modulates positional representations in early visual cortex. In our experiments, adaptation to illusory line is preserved even when abutting gratings are perceptually aligned so we could suggest that the positional shift induced by static MAE does not modulate positional representations in early visual areas such as V2 [17] and V1 [3,14], which are involved in illusory contour processing, and thereby neurons or neural populations in V1 and V2 could encode the 'misaligned abutting gratings' even when these gratings are perceptually aligned.

Dissociation between the position effects from the MAE and the processing of illusory contours might be explained by assuming different neural substrates for them. Further imaging or neurophysiological investigations are needed to clarify if the positional shift induced by static MAE is encoded somewhere higher than V1 and V2 areas.

Adaptation to illusory line in the main conditions of our experiments is preserved although subjects do not have explicit conscious access to the illusory line in the SPA phase. Therefore, activation of neurons in the visual areas involved in illusory contour processing is not strictly correlated with conscious perception [11].

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