

# Surround-contingent tilt aftereffect

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**We investigated whether aftereffects can be contingent on surroundings. Gabor patches tilted clockwise and counterclockwise were presented in alternation. Each patch was surrounded by an open circle or an open square. After prolonged exposure to these stimuli, tilt aftereffects were found to be contingent upon the surrounding frames: Vertical test patches appeared tilted clockwise when surrounded by the frame that was presented in conjunction with the adaptation patch tilted counterclockwise. The effect lasted 24 hours and was observed only when adaptation and test stimuli were presented at the same retinotopic position, but not observed at the same spatiotopic position. These results indicate that the aftereffect would be influenced not only by stimulus features but also by their surroundings.**

In these contingent aftereffects, paired two-sensory features belonged to one stimulus; the color of the grating was contingent upon the orientation of the same grating. However, the perception of a visual object is greatly influenced not only by stimulus features belonging to the object itself but also by its surroundings. For instance, the perceived brightness and color of an object are depending upon its surrounds (Albright & Stoner, 2002). The perceived shape of an object is also influenced by its surrounds (Kaufman, 1979). Adaptation to stimulus features might be affected by spatial contexts. Indeed, we found tilt aftereffects (TAE) could be contingent on the features of surrounding frames, and the effects lasted for 24 hr.

## Introduction

After prolonged exposure to pairs of different sensory features, one of the features comes to influence perception of the other feature. For example, after exposure to repeated alternations of red vertical and green horizontal gratings, a white vertical grating appears to be greenish, whereas a white horizontal grating appears to be reddish, effects which are well known as orientation-contingent color aftereffects (McCollough, 1965). A variety of contingent aftereffects have been demonstrated, such as color-contingent orientation (Held & Shattuck, 1971) and motion (Favreau, Emerson, & Corballis, 1972) aftereffects, spatial frequency-contingent (May & Matterson, 1976) and motion-contingent (Hepler, 1968) color aftereffects, and disparity-contingent motion aftereffects (Anstis & Harris, 1974). These contingent aftereffects persist for a long time, whereas simple aftereffects decay rapidly. It has been reported that contingent aftereffects persist for 24 hr (Favreau et al., 1972; Hepler, 1968) or a few days (Mayhew & Anstis, 1972).

Aftereffect has been used to study the reference frame of visual coding. The strongest tilt aftereffect is observed in the retinotopic reference frame, that is, when adaptation and test stimuli are presented in the same retinal location. However, it has been recently reported that the tilt aftereffect is remapped around the time of a saccade to remain aligned to the adapting location in the external world (Melcher, 2005, 2007; Zimmermann, Morrone, Fink, & Burr, 2013), although it has also reported that the tilt aftereffect is exclusively retinotopic (Knapen, Rolfs, Wexler, & Cavanagh, 2010; Mathôt & Theeuwes, 2013). Similarly, in other features such as motion (Ezzati, Golzar, & Afraz, 2008) and faces (Melcher, 2005), spatiotopic aftereffects have been reported, but they have been disputed subsequently (Afranz & Cavanagh, 2009; Knapen, Rolfs, & Cavanagh, 2009). To examine the reference frame of the contingent tilt aftereffect, we conducted experiments with four reference frame conditions: Position of adaptation and test stimuli were the same in retinotopic frame of reference (retinotopic), the same in spatiotopic frame of reference (spatiotopic), the same in both frames of reference (full), and different in both frames of reference (unmatched).

Citation: Nakashima, Y. & Sugita, Y. (2014). Surround-contingent tilt aftereffect. *Journal of Vision*, 14(14):5, 1–6, <http://www.journalofvision.org/content/14/14/5>, doi:10.1167/14.14.5.

## Methods

### Participants

Fourteen participants (20–26 years old) took part in the experiment, all of whom had normal or corrected-to-normal vision. The participants except the authors were naive to the purpose of the experiments. Informed consent was obtained for all participants.

### Stimuli

Two-dimensional visual stimuli were presented on a 24-inch CRT display ( $800 \times 600$  pixel resolution, refresh rate of 60 Hz) with a viewing distance of 1 m. Both adapting and test stimuli were sinusoidal luminance modulation with a spatial frequency of 4.0 cycles/°, maximum contrast, a linear envelop, a phase of 0°, and a radius of  $2.0^\circ$  presented on a uniform gray background ( $25.04 \text{ cd/m}^2$ ).

### Procedure

The participants were asked to keep looking at a red fixation ( $27.95 \text{ cd/m}^2$  and  $0.3^\circ$  in diameter) in a dark room. The fixation was presented at the center of the screen.

In the adaptation phase, adapter stimuli rotated clockwise and counterclockwise by  $15^\circ$  from a vertical orientation were presented in alternation (Figure 1A). The center of the adapter stimulus was  $2.3^\circ$  to the right from the fixation. The duration of each adapter stimulus was 3000 ms. For half of the participants, a square frame ( $3.6^\circ$  in the inner side and  $4.0^\circ$  in the outer side) was always presented in conjunction with the adapter stimulus rotated clockwise and a circle frame ( $3.8^\circ$  in inner diameter and  $4.2^\circ$  in outer diameter) in conjunction with the adapter stimulus rotated counterclockwise. For the remaining half, the relationship was reversed. The alternate presentation of the adaptation stimuli lasted for 3 min and repeated 10 times with a short rest (less than 20 s). Thus, total adaptation time was at least 30 min. In the test phase, the test stimulus was presented at  $2.3^\circ$  to the right from the fixation, the duration of which was 50 ms. In a clockwise frame condition, the test stimulus was presented in conjunction with the frame that was accompanied with the clockwise tilted adapter in the adaptation condition. In a counterclockwise frame condition, the test stimulus was presented with the frame that was accompanied with the counterclockwise tilted adapter. The no-frame condition was also included. The test stimulus was rotated by  $-2.5^\circ$  to  $2.5^\circ$

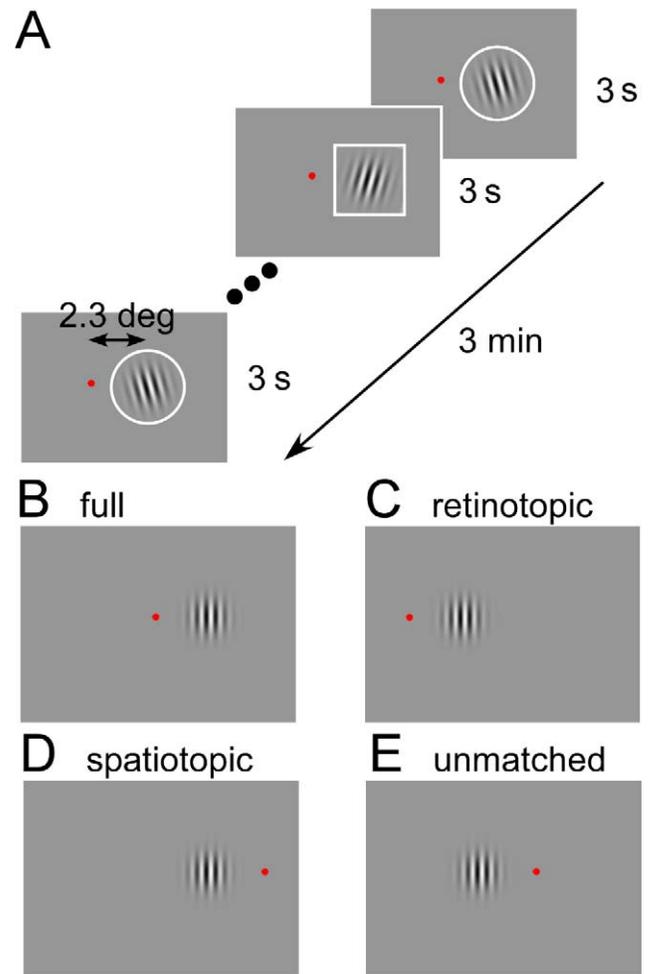


Figure 1. Stimulus image and experimental conditions. (A) In adaptation phase, adapter stimuli rotated clockwise and counterclockwise were presented for 3000 ms in alternation. The presentation lasted for 3 min. In the test phase, test stimulus, rotated by  $-2.5^\circ$  to  $2.5^\circ$  in steps of  $0.5^\circ$ , was presented for 50 ms. The test stimulus was presented in conjunction with the clockwise frame, counterclockwise frame, or no-frame. The test was conducted in the four reference frame conditions: the (B) full, (C) retinotopic, (D) spatiotopic, and (E) unmatched conditions.

from a vertical orientation in steps of  $0.5^\circ$ . The amount of rotation and the condition were randomized from trial to trial. The participants were asked to judge whether the stimulus was rotated clockwise or counterclockwise. Ten responses were obtained for each condition. The test phase was conducted before and after adaptation with the same procedure.

In the test condition mentioned above, the test stimulus was presented not only in the identical retinal location but in the same screen location (full condition). To examine the reference frame of the surround-contingent aftereffects, the participants were given another three sessions to test in another retinal position as well as in another screen position. In the retinotopic

condition, the red fixation was presented at  $5.2^\circ$  left from the screen center and the test stimulus was presented at  $2.3^\circ$  to the right from the fixation, so that the adapter and test stimuli were presented at the same retinal location but at the different screen location (Figure 1C). In the spatiotopic condition, the red fixation was presented at  $4.6^\circ$  right from the screen center and the test stimulus was presented at  $2.3^\circ$  to the left from the fixation, so that the adapter and test stimuli were presented at the same screen location but at the different retinal location (Figure 1D). In the unmatched condition, the red fixation was presented at  $2.3^\circ$  right from the screen center and the test stimulus was presented at  $2.3^\circ$  to the left from the fixation, so that the adapter and test stimuli were presented at the different retinal and screen location (Figure 1E).

To examine the persistence of the aftereffect, the test session was also conducted 1, 2, 4, 24, and 48 hr after the adaptation. Only the full condition was examined, because the strongest effect has been observed in the full condition.

## Results

Before the exposure to the adaptation stimuli, surrounding frames did not affect tilt judgments. However, the frames began to affect the perception of orientation after the exposure (Figure 2A). The vertical test pattern appeared tilted counterclockwise when presented in conjunction with the frame that was accompanied with the adaptation stimulus tilted clockwise, and appeared tilted clockwise when presented in conjunction with the frame that was accompanied with the adaptation stimulus tilted counterclockwise. To determine a point of subjective verticality (PSV), we estimated the 50% point (the point of subjective equality) by fitting a cumulative normal-distribution function to each individual's data using a maximum likelihood curve fitting technique. To evaluate the effect of adaptation, the PSV shift was calculated by subtracting the PSV for the no-frame condition from that for each frame condition. The magnitude of contingent aftereffect was obtained by subtracting the PSV shift in the pretest from that in the posttest and by averaging the PSV shift for clockwise and counterclockwise frame conditions, after the sign of the PSV shift of counterclockwise frame condition was reversed. As can be seen in Figure 2B, the surround-contingent aftereffect was observed in the full and in the retinotopic conditions. However, the effect was not observed at all in the spatiotopic and in the unmatched conditions. Before the adaptation, the PSV was not larger than the value of 0 ( $t_{13} = 0.68$ ,  $p = 0.26$ ). After adaptation, the significant PSV shift was ob-

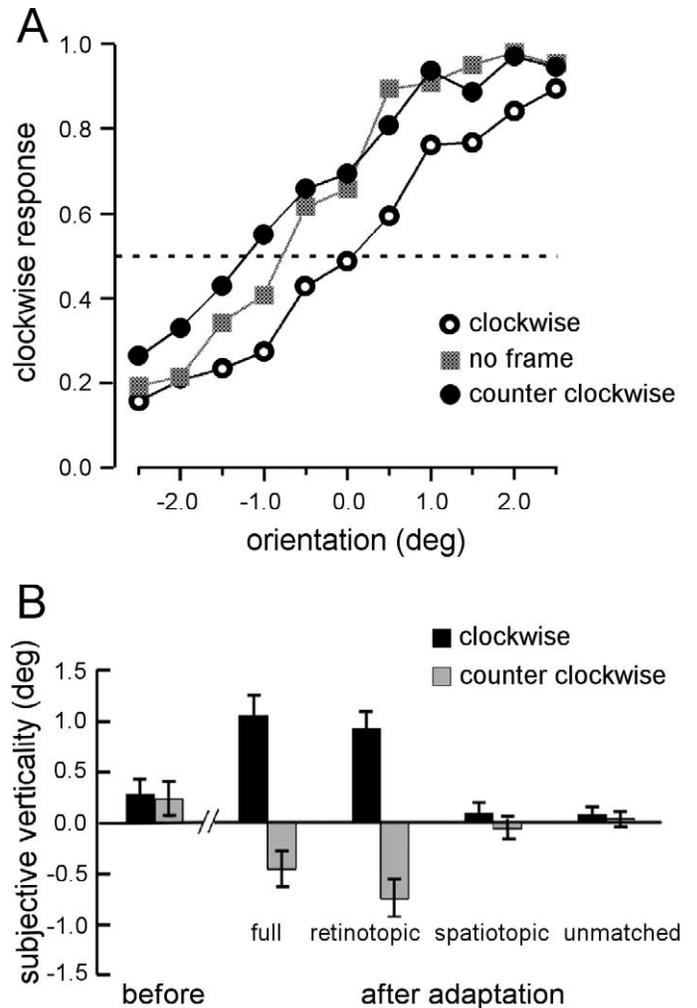


Figure 2. Magnitude of the frame-contingent aftereffect. (A) Judgments after adaptation in the full condition. Average proportion of clockwise tilt response as a function against orientation of test stimuli. (B) The shift of points of subjective verticality (PSV) in the pre- and posttest. Positive values represent the shift of PSV in the direction of the clockwise tilt. Error bars indicate the standard error.

served in the full condition ( $t_{13} = 5.80$ ,  $p < 0.01$ ) and in the retinotopic condition ( $t_{13} = 7.33$ ,  $p < 0.01$ ) but not in the spatiotopic condition ( $t_{13} = 0.75$ ,  $p = 0.23$ ) nor in the unmatched condition ( $t_{13} = -0.04$ ,  $p = 0.52$ ).

The PSV shift in the full condition declined over time. To examine the decay process of the aftereffect, the test session was also conducted 1, 2, 4, 24, and 48 hr after the adaptation. The results were plotted on log-log coordinates (Figure 3). The magnitude of aftereffect appeared to decay linearly. A straight line correlated well to the data with an  $R^2$  value of 0.916, and the slope was  $-0.24$ . The significant aftereffect was still observed 24 hr after adaptation ( $t_6 = 2.57$ ,  $p < 0.05$ ). These results indicate the surround-contingent tilt aftereffect lasted for 24 hours.

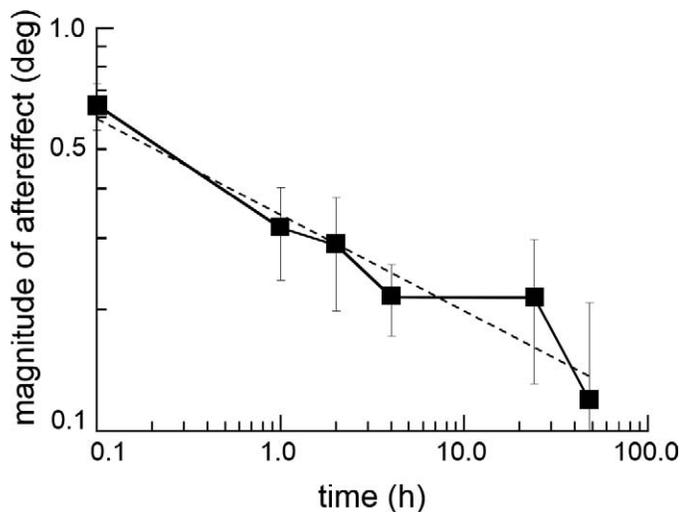


Figure 3. The magnitude of contingent aftereffect as a function of time after adaptation. The posttest was conducted immediately, 1, 2, 4, 24, and 48 hr after adaptation. Error bars indicates the standard error.

## Discussion

We found that tilt aftereffects could be contingent upon the shape of surrounding frames. After the exposure to Gabor patches tilted clockwise and counterclockwise surrounded by a circle or a square frame, vertical test patches appeared tilted clockwise when surrounded by the frame that was presented in conjunction with the adaptation patch tilted counterclockwise and vice versa. The effect was observed only when adaptation and test stimuli were presented at retinotopically the same position, but not observed when they were presented at the same spatiotopic position. The effect lasted at least for 24 hours.

The contingent tilt aftereffects have been demonstrated for such a stimulus that contained both test and induction stimulus features. For example, in the color-contingent orientation aftereffect, the orientation of the grating is contingent on the color of the same grating (Held & Shattuck, 1971). The present study demonstrated that the tilt aftereffect could be contingent upon an induction stimulus presented in the outside of the test stimulus. It has been generally thought that contingent aftereffects require joint encoding of the parameters to be linked (Barlow, 1990; Braddick, Campbell, & Atkinson, 1978). It is now well known that the perception of a visual object is greatly influenced not only by stimulus features belonging to the object itself but also by its surroundings. Correspondingly, the activity of cortical visual cells is strongly modulated by stimuli presented outside of their receptive fields (Blakemore & Tobin, 1972; Gilbert & Wiesel, 1990; Knierim & van Essen, 1992; Lamme,

1995; Sillito, Grieve, Jones, Cudeiro, & Davis, 1995). These cells might be responsible for the surrounds-contingent aftereffects. The information of surrounding frames would modulate the activities of the cells that were responding to the Gabor patch. The orientation and the frame shape information might be associated.

It has been reported that motion and texture density aftereffects are contingent on the color of the surrounds (Durgin, 1996; Potts & Harris, 1975; Sharpe, Harris, Fach, & Braun, 1991). This color-contingent aftereffect was thought to be mediated by color spreading in the retina (Poppel, 1986). In the present study, the aftereffect was contingent on arbitrary shapes of frames that are processed in the cortex. The frame shape-contingent aftereffect is likely to be accounted by interactions between cells in the visual cortex.

Contingent aftereffects are well known for their long-lasting effects. The present study confirmed that the surround-contingent tilt aftereffect lasted at least for 24 hr. It is certainly possible that the outside frames simply biased the participants' responses and that frame information was utilized for making decisions only when the orientation was difficult to discriminate. To examine this possibility we calculated the slope of psychometric function with the following formula:  $(75\% \text{ threshold} - 25\% \text{ threshold})/2$ . However, we found no significant differences for any comparison of conditions or time points, indicating the aftereffect cannot be explained by the response bias alone.

It has been shown that visual contingent aftereffects were largely monocular and specific to retinal position. Stromeyer (1972) found that the McCollough effect was not observed when the test gratings were moved off the adapted retinal area. Color-dependent motion aftereffect was shown to be highly localized (Murch, 1974). Frame-dependent tilt aftereffect was also highly localized: The effects were observed only when adaptation and test were presented at the same retinal position. These results suggest that the aftereffect would be mediated in the relatively early stage of the visual processing.

Some studies reported that tilt aftereffect occurs in a spatiotopic frame of reference (Melcher, 2005, 2007; Zimmermann et al., 2013), whereas other studies claimed that it is not spatiotopic but retinotopic (Knapen et al., 2010; Mathôt & Theeuwes, 2013). Our results showed that tilt aftereffect is retinotopic even when it is contingent on the surroundings. However, we presented adapting and test stimuli in the different hemi-field in the spatiotopic condition. The aftereffects might be observed if these stimuli were presented in the same hemi-field. Thus, we cannot conclude that the reference frame of simple tilt aftereffect is exclusively retinotopic.

*Keywords:* adaptation, tilt aftereffect, contingent aftereffect, reference frame

## Acknowledgments

This work was supported by Grant-in-Aid for Scientific Research (25245069), Japan Society for the Promotion of Science (JSPS). Principal Investigator: Yoichi Sugita.

Commercial relationships: none.

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