

# Stereoscopic depth aftereffects without retinal position correspondence between adaptation and test stimuli

Shuichiro Taya <sup>a,\*</sup>, Masayuki Sato <sup>b</sup>, Sachio Nakamizo <sup>a</sup>

<sup>a</sup> Department of Psychology, Kyushu University, 6-19-1, Hakozaki, Higashiku, Fukuoka 812-8581, Japan

<sup>b</sup> Faculty of Environmental Engineering, The University of Kitakyushu, 1-1, Hibikino, Wakamatsuku, Kitakyushu 808-0135, Japan

Received 19 July 2004; received in revised form 20 January 2005

## Abstract

To clarify whether stereo-slant aftereffects are independent of stimulated retinal position, two experiments compared the magnitude of aftereffects between the following two conditions: when the adaptation and test stimulus fell on (1) the same retinal position, and (2) on different retinal positions separated by 0.5°–20°. In Experiment 1, disc- or ring-shaped surface consisting of random-dots was presented at the central or peripheral visual fields. In Experiment 2, rectangular surface was presented at the upper or lower visual fields. After two minutes inspection of a random-dot stereogram depicting a ±30° slanted surface, the observer adjusted the slant of the test stimulus to appear fronto-parallel. The results of the experiments showed that significant aftereffects were observed similarly in both conditions. Moreover, the separation nor the stimulus shape scarcely affected the magnitude of the aftereffects. Based on these results we concluded that the depth processing mechanism which operates independently from the stimulated retinal position is responsible for the depth aftereffects we found.

© 2005 Elsevier Ltd. All rights reserved.

**Keywords:** Adaptation; Aftereffect; Stereopsis; Retinal-position dependency; Depth perception

## 1. Introduction

A few minutes inspection of a three-dimensional (3D) stimulus alters the apparent depth of a subsequently presented stimulus. For example, after inspecting a surface slanted in depth, objectively frontal surfaces appear slanted in the opposite direction of the inspected surface.<sup>1</sup> Such alterations in apparent depth as a result of

adaptation to 3D stimuli are called depth aftereffects (for a recent review, see Howard & Rogers, 2002).

Previous studies have shown that depth aftereffects occur only when an observer fixes their gaze so that adaptation and test stimuli fall on the same retinal position (Köhler & Emery, 1947; Mitchell & Baker, 1973). For example, Mitchell and Baker (1973) examined the effects of retinal separation between adaptation and test stimuli (vertical bar) on the magnitude of depth aftereffects. They showed that aftereffects decreased with increasing separation, almost disappearing when the separation was over 10 arcmin (see Mitchell & Baker, 1973, Fig. 4). As the results suggest, depth aftereffects are generally retinal position-dependent (Blakemore & Julesz, 1971; Howard & Rogers, 2002; Köhler & Emery, 1947; Mitchell & Baker, 1973; Rose & Price, 1995).

In contrast, some studies have shown that depth aftereffects occur even when the observer actively moves

\* Corresponding author. Tel./fax: +81 92 642 2418.

E-mail address: [taya@psycho.hes.kyushu-u.ac.jp](mailto:taya@psycho.hes.kyushu-u.ac.jp) (S. Taya).

<sup>1</sup> The term “slant” has been used often to represent an inclination on a two-dimensional plane as well as an inclination in a three-dimensional space. Here this term is used to represent an inclination in depth after the examples of many other studies (e.g. Seyama, Takeuchi, & Sato, 2000).

their gaze, and especially when the adaptation stimulus was a slanted surface (slant aftereffects: Bergman & Gibson, 1959; Ryan & Gillam, 1993; Wenderoth, 1970). For example, Bergman and Gibson (1959) compared the magnitude of slant aftereffects with- and without-fixation conditions. They showed that the magnitude of slant aftereffects were almost equivalent under the two conditions. The results suggest the possibility that slant aftereffects are not always retinal position-dependent.

Whether the slant aftereffects are independent of retinal position remains unclear. Previous studies (e.g., Bergman & Gibson, 1959) have not provided definite evidence that slant aftereffects are retinal position-independent, because under the without-fixation adaptation condition the position of retinal stimulation cannot be identified. Therefore under such experimental conditions, the adaptation and test stimuli are likely to fall on the same retinal position, and in this case, slant aftereffects are position-dependent. To examine whether slant aftereffects are retinal position-independent, we have to observe the aftereffects under a condition that fulfills the following criterion: the observers must keep their gaze on a fixation point during the adaptation and test period so that these stimuli definitely fall on different retinal positions.

This study had two goals. First, to examine whether slant aftereffects are independent of retinal position under a controlled condition that fulfills the above-mentioned criterion (Experiment 1). Second, to examine whether the shape of the stimulus surface is critical for the position-dependency of the slant aftereffects (Experiment 2). The magnitudes of the aftereffects were measured under the following two adaptation conditions: the adaptation and test stimuli were presented (1) at the same retinal position and thus overlapping (*overlap condition*), and (2) at different retinal positions and thus not overlapping (*separate condition*). In both conditions the observers were required to maintain a fixed gaze during the adaptation and test period.

## 2. Experiment 1

The purpose of this experiment was to examine whether slant aftereffects are retinal position-independent. The stimuli consisted of a disc- and ring-shaped random-dot stereogram depicting a surface slanted about a vertical axis. The inner-diameter of the ring was always larger than the diameter of the disc and they were presented successively in a concentric fashion; therefore, when the adaptation stimulus was a ring and the test stimulus was a disc (or vice versa) these stimuli did not overlap (separate condition). If aftereffects occur in this condition, it suggests that the slant aftereffects are retinal position-independent.

### 2.1. Methods

#### 2.1.1. Observers

Four observers participated in this experiment. Observer MS and ST were the authors, and observers SK and YI were naïve with respect to the purpose of the study. They all had normal or corrected to normal visual acuity and also normal stereo acuity confirmed by a Randot stereotest.

#### 2.1.2. Apparatus and stimuli

The adaptation and test stimuli were central disc-shaped and surrounding ring-shaped surfaces (Fig. 1). They formed the stereo-pair of a 1.2% random-dot pattern depicting a flat surface slanted about a vertical axis. The random-dot pattern was generated using a Cambridge Research Systems VSG 2/5 graphics card in a host Windows computer and rear projected onto a 100-in. screen by a cathode-ray-tube (CRT) projector (Christie Digital Systems, Marquee8500/3D). The dichoptic half-images were selectively presented to each eye of each observer through a liquid crystal shutter goggles (Cambridge Research Systems, FE-1). The goggles were fixed on a metal frame placed in front of the observation seat and served as a headrest. The frame rate of the projector was 120 Hz thus the effective frame rate to each eye was 60 Hz. There was no noticeable flicker at this frame rate and no visible crosstalk between the two half-images. The experimental room was carefully darkened so that the observer saw nothing but the stimulus throughout the experiment. The fixation point was rear-projected onto the center of the screen by a laser pointer. Viewing distance was 115 cm. At this viewing distance, 1 pixel subtended  $5.8 \times 5.8$  arcmin. An anti-aliasing technique was used to reduce the pixelation problem. Dot luminance measured through the goggle was  $5.5 \text{ cd/m}^2$ ; the effective luminance value was half of this because the shutter was closed half the time during observation.

#### 2.1.3. Adaptation conditions

The overlap and separate conditions were compared to quantify adaptation efficiency as a function of retinal position. In the overlap condition, the disc was presented at the same retinal position during both the adaptation and test period. This condition was labeled the CC (Center–Center) condition. The separate condition consisted of two sub-conditions labeled the SC (Surround–Center) and CS (Center–Surround) conditions. In the SC condition, the ring and disc were presented during the adaptation and test periods, respectively, while in the CS condition, the disc and ring presentation was reversed.

In the separate condition, there was a gap between the adaptation and test stimuli. The size of the gap in the separate condition was also manipulated. Three

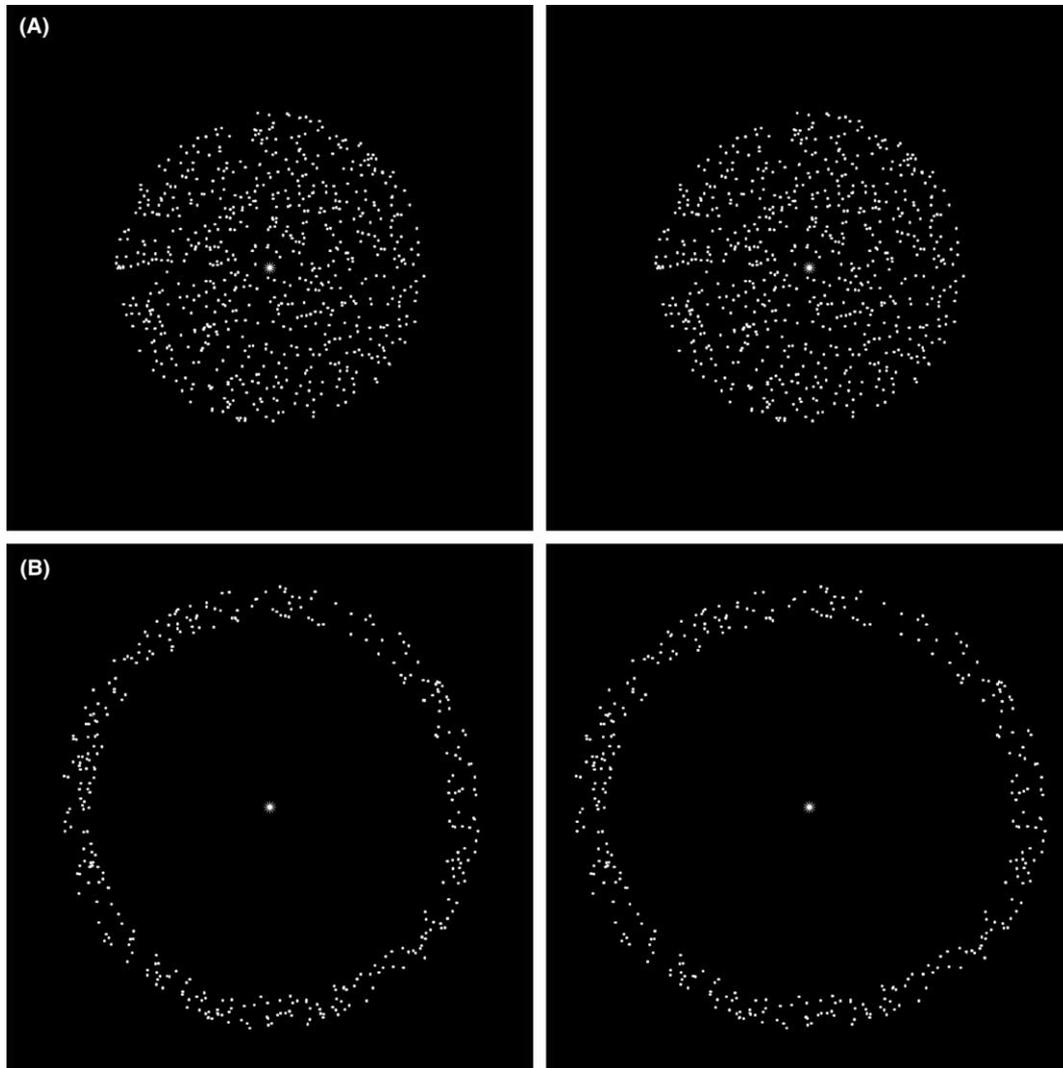


Fig. 1. Example of the stimuli in Experiment 1. Stereo-pair (A) specifies a fronto-parallel surface whereas stereo-pair (B) specifies a surface slanted about a vertical axis. After binocularly fusing stereo-pair (B) for 120 s (holding fixation on at the central fixation point), (A) appears slanted in a direction opposite to (B).

gap sizes were constructed by varying the diameter of the disc stimuli to 26°, 21°, and 11°. The outer and inner diameters of the ring were fixed at 36° and 31°. Consequently, when the diameter of the disc was 26°, 21°, and 11°, the gap size was 2.5°, 5°, and 10°, respectively. To compare the magnitude of the aftereffects, the diameter of the disc presented in the CC condition was also varied between 26°, 21°, and 11°.

#### 2.1.4. Procedure

To quantify the magnitude of the aftereffects, a nulling task was adopted. The observers' subjective frontal surfaces were measured by the method of adjustment. The adjusted slant values were compared before and after adaptation.

In the pre-adaptation trial, the observer adjusted the test stimulus without adaptation to establish a baseline for each observer. The test stimulus, either the disc or

ring, was presented in the center of the screen and the observer was asked to adjust the slant of the test stimulus by pressing two buttons until it appeared in a fronto-parallel plane while maintaining their gaze on the fixation point. The initial slant was selected randomly from a range of  $-15^\circ$  to  $+15^\circ$  (a positive value indicates the right side away). The slant of the test stimulus was varied by  $1^\circ$  by pressing the button once. The mean of the nine settings for each stimulus pattern (disc or ring) were used as the baseline for calculating the magnitude of the aftereffects.

In the adaptation trial, the observer initially inspected the adaptation stimulus for two minutes. The simulated slant of the adaptation stimuli was set at either  $-30^\circ$  or  $+30^\circ$ . During both the adaptation and test periods, the observers were asked to keep their gaze on the fixation point to assure that the stimulus was presented to the proper restricted retinal position. The position of the

dots on the stimulus surface changed randomly every 10 s to prevent dot afterimages. After the initial adaptation period, alternative 5 s presentations of the test stimulus and 10 s re-presentation of the adaptation stimulus followed. This stimulus presentation method was adopted to prevent the aftereffects from decreasing during slant adjustment (Graham & Rogers, 1982). The initial slant of the test stimulus was selected randomly from a range of  $-15^\circ$  to  $+15^\circ$ . The observers' task was to adjust the slant of the test stimulus so that it appeared frontal during the test stimulus presentation. Alternation of the test and adaptation continued until the observer was satisfied, at which point another button was pressed to finish the setting. Before initiating the next different adaptation condition, a break of more than 5 min was taken to assure that the aftereffects of the previous adaptation had sufficiently disappeared. This was confirmed by checking that observers' apparently-frontal stimulus settings between the different adaptation conditions were close to their pre-adaptation values. In total, each observer carried out 108 slant adjustments (3 [adaptation conditions: CS, SC, and CC]  $\times$  3 [disc diameter (gap in the separate condition):  $26^\circ$ ,  $12^\circ$ , and  $11^\circ$  ( $2.5^\circ$ ,  $5^\circ$ , and  $10^\circ$ )]  $\times$  2 [adaptation slant:  $-30$  and  $+30^\circ$ ]  $\times$  6 [repetition]).

## 2.2. Results and discussion

The magnitudes of the aftereffects were calculated by subtracting the baseline from the frontal settings after each adaptation. Fig. 2 shows the group mean of the aftereffects averaged over four observers.

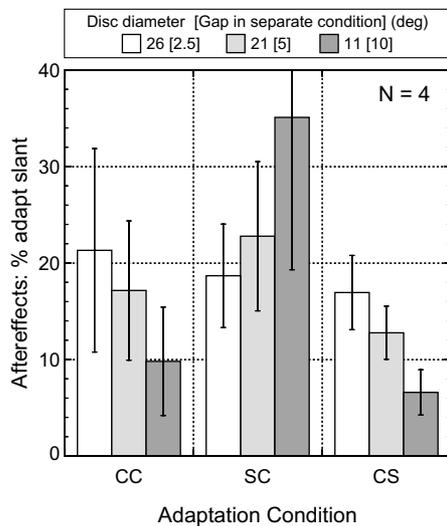


Fig. 2. Group means in Experiment 1. The ordinate shows the magnitude of the aftereffects (percent) against the slant of the adaptation stimulus ( $\pm 30^\circ$ ). The abscissa shows the adaptation condition. White, light gray and dark gray represent the diameters of the discs, or the sizes of the gaps between adaptation and test stimuli under separate conditions (parenthetic figures). Error bars show  $\pm 1$  standard errors.

Almost all the aftereffects significantly differed from zero at the 95% confidence limit. Table 1 shows the individual means averaged over the 12 trials, the 95% confidence intervals calculated from the standard deviation for each observer and each sub-condition, and also the group mean averaged across the four observers and the 95% confidence interval for the group mean. In the group mean, significant aftereffects were observed in the all sub-conditions except for the smallest disk size of the CC condition (i.e. disk diameter =  $11^\circ$ ). Under this condition, the significant aftereffects were observed for MS and SK, but the aftereffect for ST and YI were non-significant. ST and YI claimed they could barely perceive the slant of the smallest disc. Previous studies have reported that some observers have low sensitivity to the slant of a single surface defined by disparity gradient (Sato & Howard, 2001). Probably, ST and YI were this type of observer; therefore they might have found it hard to perceive the slant of the smallest disk. Consequently, data of ST and YI could have affected the overall group data.

We performed two way repeated-measures analysis of variance (ANOVA) on the magnitude of aftereffects with the factor of the adaptation condition and the diameter of the disk.<sup>2</sup> The main effect of the adaptation condition and the diameter of the disk was not significant ( $F_{2,4} = 0.68$ ,  $p = 0.56$  and  $F_{2,4} = 1.16$ ,  $p = 0.40$ , respectively). The results of ANOVA revealed that the difference between adaptation conditions did not systematically affect the magnitude of aftereffects. The magnitude of aftereffects did not significantly differ among the three adaptation conditions (CC, SC, and CS). Moreover, gap size scarcely affected the magnitude of aftereffects. The individual data (Table 1) also show that there was no consistent tendency such that the magnitude of aftereffects obtained from the overlap condition was always larger than that obtained from the separate conditions (or vice versa). Also there was no consistent tendency such that the smaller (or larger) disk sizes produced greater aftereffects.

These results suggest that slant aftereffects are not dependent on the stimulated retinal position at least when the observers have adapted to the disparity-defined slanted surface. Significant aftereffects were observed even when the position of the adaptation and test stimuli were separated by a gap of  $2.5^\circ$ – $10^\circ$ . These results are incongruent with the previous research,

<sup>2</sup> YI's data were partly lacking in the condition in which the smallest size of the disc was used as test stimulus (i.e. CS and SC), because YI could not perceive the slant of the smallest disc at all. Therefore, the data from the remaining three observers were used for the ANOVA.

Table 1  
The individual data of Experiment 1

Observer	Mean			95% confidence interval		
	CC	SC	CS	CC	SC	CS
<i>Diameter of the disc = 26° (Gap size = 2.5°)</i>						
M.S.	10.28	3.89	13.89	13.78	2.61*	3.64*
S.K.	26.67	29.44	25.28	9.20*	5.68*	5.25*
S.T.	48.33	19.72	7.78	6.72*	20.37	3.91*
Y.I.	0.00	21.67	20.83	14.42	9.42*	12.66*
Group mean	21.32	18.68	16.94	20.67*	10.50*	7.55*
<i>Diameter of the disc = 21° (Gap size = 5°)</i>						
M.S.	10.28	3.06	13.89	13.17	3.98	4.89*
S.K.	26.67	23.06	16.94	5.43*	6.65*	8.05*
S.T.	31.39	40.83	15.56	14.13*	10.21*	8.05*
Y.I.	0.28	24.17	4.72	9.61	9.49*	18.35
Group mean	17.15	22.78	12.78	14.15*	15.15*	5.40*
<i>Diameter of the disc = 11° (Gap size = 10°)</i>						
M.S.	16.11	11.39	6.94	4.18*	3.46*	3.48*
S.K.	14.72	28.89	13.06	13.65*	6.53*	5.60*
S.T.	-1.39	65.00	3.89	20.24	18.76*	17.57
Y.I.	-	-	2.50	-	-	17.42
Group mean	9.81	35.09	6.60	11.01	30.94*	4.59*

Note: CC, center-center condition; SC, surround-center condition; CS, center-surround condition.

\*  $p < .05$ .

which showed that depth aftereffects are retinal position-dependent (Köhler & Emery, 1947; Mitchell & Baker, 1973).

At this point, whether or not the shapes of the stimulus surface were critical for the present results was unknown; that is, whether a stereoscopic surface interpolation was responsible for the position-independent slant aftereffects found in this experiment. Previous studies have shown that the visual system often interpolates the depth between two separated stereoscopic surfaces, constructing an implicit surface representation (e.g. Wilcox & Duke, 2003). Therefore, under the SC condition, the observers likely adapted to the slant of an implicit surface subjectively interpolated inside the ring during the adaptation period. Similarly, under the CS condition, the observers likely used the implicit surface inside the ring as the test stimulus for the slant adjustments. Ryan and Gillam (1993) demonstrated that such implicit surfaces effectively serve as adaptation and test stimuli; although they did not control the fixation point.

### 3. Experiment 2

In this experiment a horizontally elongated rectangular surface was presented in the upper or lower visual field of the observers as shown in Fig. 3. In contrast with the ring-shaped stimulus in Experiment 1, the interpolated surface did not serve as the adaptation and test

stimuli with this stimulus shape and arrangement. Consequently, if the position-independent slant aftereffects can be solely attributed to the interpolated surface, no aftereffects should occur under the separate condition during Experiment 2.

#### 3.1. Methods

##### 3.1.1. Observers

Six observers participated in this experiment. Three (MS, SN and ST) were the authors, and the others (HA, HM and SO) were naïve with respect to the purpose of the experiment. They all had normal or corrected to normal visual acuity and normal stereo acuity confirmed by a Randot stereotest.

##### 3.1.2. Apparatus and stimuli

The adaptation and test stimuli were horizontally elongated rectangular random-dot surfaces (Fig. 3). They were 1.2 % random-dot pattern depicting a flat surface slanted about a vertical axis. They were presented above or below the fixation point, which was projected at the center of the screen by a laser pointer. Instead of the goggles used in Experiment 1, a different liquid crystal goggles (Stereographics, Crystal Eyes2) were used to provide a larger visual field. A chin-rest was used to restrict the observers' head movements. All other conditions were the same as in Experiment 1.

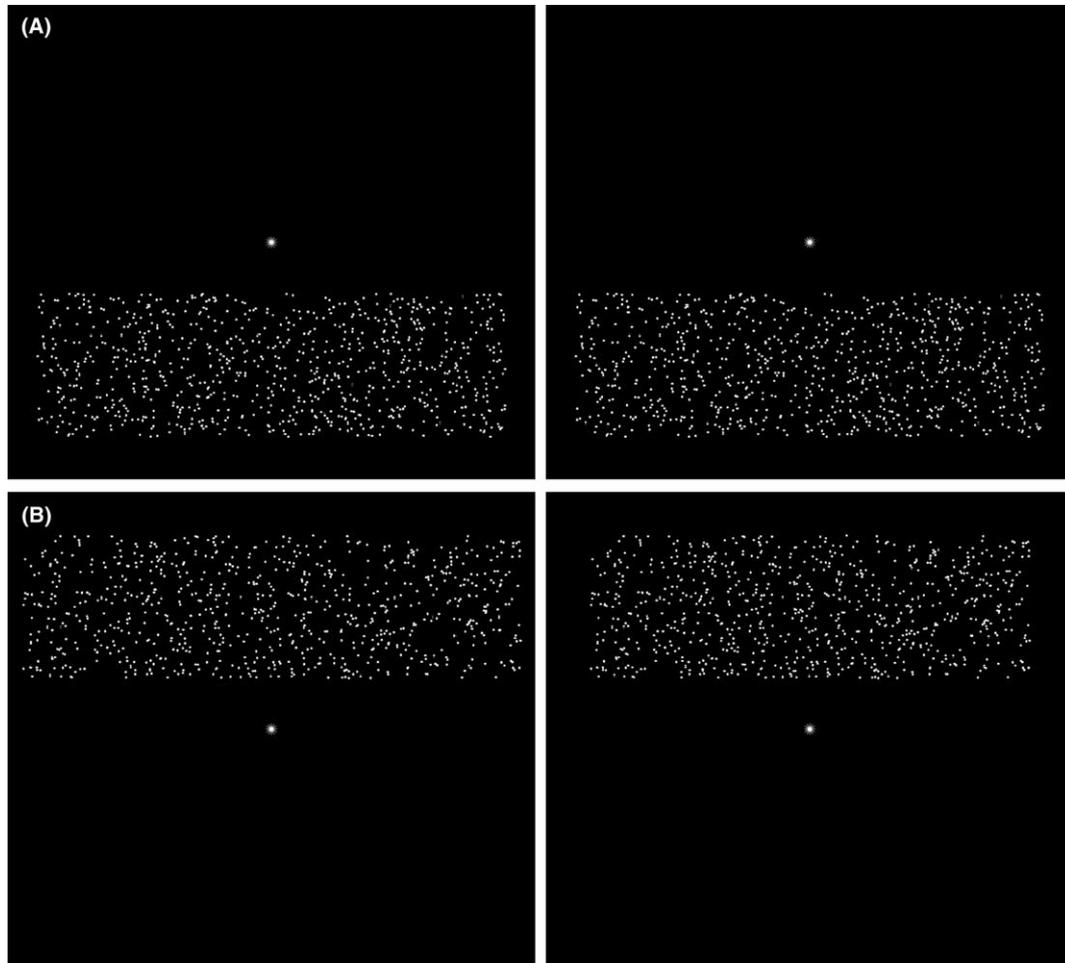


Fig. 3. Example of the stimuli in Experiment 2. Stereo-pair (A) specifies a fronto-parallel surface whereas stereo-pair (B) specifies a surface slanted about a vertical axis. After binocularly fusing stereo-pair (B) for 120 s (holding fixation on at the central fixation point), (A) appears slanted in a direction opposite to (B).

### 3.1.3. Adaptation conditions

The magnitude of aftereffects between the overlap and separate conditions were once again compared. The slant of the adaptation stimuli and initial slant of the test stimuli were the same as that described for Experiment 1. In the overlap condition, both the adaptation and test stimuli were presented at the upper or lower visual field of the observer. In the separate condition, the adaptation stimulus was presented at the upper area of the visual field then the test stimulus was presented at the lower area of the visual field (or vice versa). Therefore, in the separate condition, there was a gap between the adaptation and test stimuli.

In the separate condition, three gap sizes were set-up by varying the height of the rectangles. When the height of the rectangles was 17.75°, 13°, and 8° the gap size was 0.5°, 10°, and 20°, respectively. To compare the magnitude of the aftereffects, the height of the rectangle presented in the overlap condition was also varied between 0.5°, 10°, and 20°. The width of the rectangles was always 47°.

### 3.1.4. Procedure

The procedure was the same as that described for Experiment 1 except for the stimulus configuration and arrangement. The observers were again asked to keep their gaze on the fixation point during the adaptation and test period. In total, each observer carried out 144 slant adjustments (2 [adaptation condition: overlapped and separated]  $\times$  2 [adaptation stimulus position: upper and lower]  $\times$  3 [rectangle height (gap in the separate condition): 17.75°, 13° and 8° (0.5°, 10°, and 20°)]  $\times$  2 [adaptation slant:  $-30^\circ$  and  $+30^\circ$ ]  $\times$  6 [repetition]).

### 3.2. Results and discussion

The magnitudes of the aftereffects were calculated in the same way as described for Experiment 1. Fig. 4 shows the group mean of the aftereffects averaged over the six observers. Table 2 shows the individual means averaged over 24 trials, the 95% confidence intervals for each observer and each sub-condition, and also the

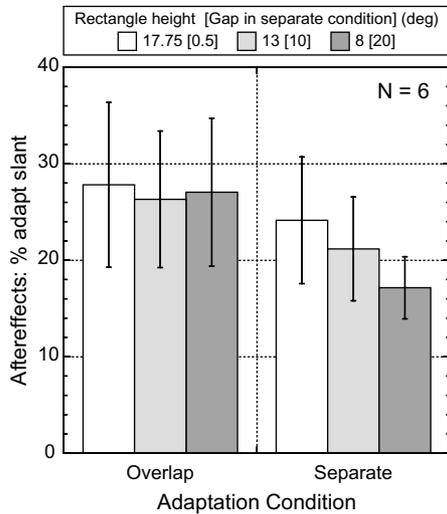


Fig. 4. Group means in Experiment 2. The ordinate shows the magnitude of the aftereffects (percent) against the slant of the adaptation stimulus ( $\pm 30^\circ$ ). The abscissa shows the adaptation condition. White, light gray and dark gray represent diameters of the discs, or the sizes of the gaps between the adaptation and test stimuli under separate conditions (parentetic figures). Error bars show  $\pm$  standard errors.

group mean averaged across the six observers and the 95% confidence interval for the group mean. Almost all the aftereffects were significantly different from zero at the 95% confidence intervals. In the group mean, all aftereffects were significantly different from zero. In the individual data, almost all aftereffects were significant with minor exceptions.

We performed two way repeated-measures ANOVA on the magnitude of the aftereffects with the factors of the adaptation condition and the height of the rectangle. The main effects of the adaptation condition and the height of the rectangle were not significant ( $F_{1,5} = 1.29, p > .1$  and  $F_{2,10} = 0.58, p > .1$ , respectively). The results suggest that the difference between adaptation conditions and gap size did not systematically affect the magnitude of aftereffects.

However, greater consideration regarding individual response patterns might be necessary for interpretation of the results. As seen in Table 2, five of the six observers showed larger aftereffects in the overlap than in the separate condition. Only observer SN showed the opposite pattern of aftereffects.<sup>3</sup> When SN is excluded from ANOVA, the effect of the adaptation condition is significant ( $F_{1,4} = 13.05, p < .05$ ), although the effect of the rectan-

Table 2  
The individual data of Experiment 2

Observer	Mean		95% confidence interval	
	Overlap	Separate	Overlap	Separate
<i>Height of the rectangle = 17.75° (Gap size = 0.5°)</i>				
H.A.	11.94	11.11	8.56*	4.14*
H.M.	20.14	17.22	7.93*	7.36*
M.S.	22.50	11.11	5.78*	4.33*
S.N.	5.14	19.72	9.08	6.64*
S.O.	55.14	52.50	29.39*	21.17*
S.T.	52.08	33.19	12.55*	7.34*
Group mean	33.72	29.13	23.59*	17.67*
<i>Height of the rectangle = 13° (Gap size = 10°)</i>				
H.A.	7.64	10.83	3.00*	3.21*
H.M.	18.47	9.58	10.24*	5.40*
M.S.	25.00	14.86	8.65*	5.59*
S.N.	12.08	24.44	8.54*	7.66*
S.O.	48.19	45.14	15.59*	20.68*
S.T.	46.53	22.22	8.25*	11.99*
Group mean	32.95	26.67	17.12*	12.72*
<i>Height of the rectangle = 8° (Gap size = 20°)</i>				
H.A.	10.14	6.81	4.22*	2.58*
H.M.	30.14	14.86	10.42*	8.83*
M.S.	34.72	15.14	8.28*	5.92*
S.N.	3.19	30.97	16.25	13.52*
S.O.	55.97	18.89	24.94*	16.27*
S.T.	28.19	16.25	6.84*	5.00*
Group mean	30.52	20.31	21.30*	7.13*

\*  $p < .05$ .

gle height remains not significant ( $F_{2,8} = 0.96, p > .1$ ). Therefore, the results could indicate that the magnitude of the aftereffects in the separate condition was significantly smaller than that in the overlap condition.

Note that the results do not indicate that the stereoscopic slant aftereffects are completely dependent on retinal position, because significant aftereffects were observed even in the separate condition. Rather, the results suggest that at least two types of aftereffects might be involved in stereoscopic slant aftereffects: retinal position-dependent aftereffects and retinal position-independent aftereffects. Probably, the aftereffects in the overlap condition were the sum of the position-dependent and position-independent aftereffects, whereas the aftereffects in the separate condition were position-independent aftereffects only. Consequently, the magnitude of aftereffects in the overlap condition was larger than that in the separate condition. We discuss the mechanism mediating these two types of aftereffects in Section 4.

It was possible that observers involuntarily moved their gaze toward the adaptation stimuli during the adaptation period. To investigate whether or not the aftereffects observed in the separate condition were the results of an accidental overlapping of adaptation and test stimuli by involuntary eye movements, we

<sup>3</sup> We are not sure why observer SN showed very small aftereffects in the overlap condition; however, a possible explanation relates to the effects of aging. In our study, only SN was over 60 years old, whereas the age of the other observers ranged from 22 to 36. It has been reported that aging affects on dark adaptation (Jackson, Owsley & McGwin, 1999). Although no study has suggested aging affects on stereoscopic adaptation, it is possible that aging has some unknown factors that could have caused the exceptional nature of SN's data.

measured the magnitude of the aftereffects while monitoring eye movements of an observer (ST) during the adaptation and test periods. The experimental procedure was the same as the separate condition with the 20° gap in Experiment 2. We monitored the observer's eye position using the electro-oculogram (EOG) technique. The results revealed that the aftereffects observed in the separate condition were not the by-product of the involuntary eye movements. The eye movements recorded confirmed that observers successfully maintained their gaze on the fixation point. Nevertheless, after two minutes adaptation, an observer's settings of the frontal plane significantly deviated in a direction opposite of the adaptation surface ( $p < .05$ ), meaning that there were significant aftereffects.

In sum, these results suggest that the position-independent slant aftereffects cannot be solely explained by the stereoscopically interpolated surface. With the stimulus shape and arrangement of Experiment 2, it is unlikely that the interpolated surface served as either the adaptation or test stimuli. Nevertheless, significant aftereffects were obtained from the separate condition in which the presented retinal position of the adaptation and test stimuli were separated by a gap. Moreover, our results did not show the effects of the gap size on the magnitude of the aftereffects.

#### 4. General discussion

The present findings suggest that depth aftereffects cannot be solely explained by the conventional models. Conventionally, depth aftereffects have been explained by the fatigue of disparity-selective neurons as a result of continuous stimulation (Berends & Erkelens, 2001; Howard & Rogers, 2002; Long & Over, 1973; Mitchell & Baker, 1973). Disparity-selective neurons are found in the lower level of visual information processing such as area V1, in which the receptive field size is considerably small (Desimone & Duncan, 1995). Therefore, although disparity-selective neurons might be responsible for the position-dependent depth aftereffects (Long & Over, 1973; Mitchell & Baker, 1973), their receptive field is too small to mediate the position-independent slant aftereffects observed here. In our study, the maximum separation between adaptation and test stimuli was 20°, considerably larger than the size of the lower level receptive fields (according to Boussaoud, Desimone, and Ungerleider (1991) the receptive field of area V4 is smaller than 5° at 10° eccentricity). Thus, the present findings suggest that the depth processing mechanism that operates independently from the stimulated retinal position is responsible for the depth aftereffects. We discuss below three explanations, all of which can potentially explain position-independent depth aftereffects. These explanations are based on assumptions that

(1) surface extrapolation, (2) neurons with large receptive fields, and (3) disparity re-calibration, respectively operate.

The first explanation is based on the assumption that the slant signal assigned in one visual field was extrapolated into the other visual field in which no slant signal had been assigned. Although we showed that the position-independent slant aftereffects cannot be solely explained by the interpolation of the slant signal between two separated surfaces (e.g. inside of the ring-shaped surface), it is not clear whether the slant signal was extrapolated outside the stimulus surface. For example when the adaptation surface was presented in the upper visual field, the slant signal of the surface might be extrapolated into the lower visual field; and then observers adapted to the extrapolated slant surface. As a consequence, the aftereffects occurred at the lower visual field at which the adaptation surface had not presented during the adaptation period.

The second explanation is based on the assumption that the fatigue of neurons with a large receptive field is responsible for depth aftereffects. Recent neuro-physiological studies have found that neurons selectively tune to slanted stimuli in the middle temporal area (Nguyenkim & DeAngelis, 2003), the caudal part of the lateral bank of the intraparietal sulcus (Tsutui, Sakata, Naganuma, & Taira, 2002), and the inferior temporal cortex (Janssen, Vogels, & Orban, 2000). These areas are much higher than the areas responsible for disparity processing. In general, receptive field size increases as the level of the visual processing becomes higher (Desimone & Duncan, 1995). It is likely that in our study neurons with large receptive fields mediated adaptation because the stimuli we used were slanted surfaces. Also, previous studies have suggested that depth adaptation occurs at a relatively higher stage, at which depth information provided by each depth cue is integrated and 3-D shape representation is achieved (Balch, Milewski, & Yonas, 1977; Bradshaw & Rogers, 1996; Domini, Adams, & Banks, 2001; Duke & Wilcox, 2003; Poom & Börjesson, 1999). Position-independent depth aftereffects might occur at this level.

The third explanation is based on the assumption that "cue conflict" in a stimulus is responsible for position-independent depth aftereffects. When depths signaled by disparity and a monocular cue are in conflict, the apparent depth is predicted as the weighted mean of the depth assigned by each depth cue (Landy, Malony, Johnston, & Young, 1995). It is known that the visual system recalibrates the relationship between disparity and apparent depth when there is a conflict (disparity recalibration: Adams, Banks, & van Ee, 2001). Some studies have suggested that depth aftereffects are the result of disparity recalibration (Adams et al., 2001; Epstein & Morgan-Paap, 1974). The disparity recalibration is probably conducted independently of

the retinal position, because in a natural scene the relationships between disparity and apparent depth are constant over the whole visual field. With the stimuli used in this study, there was a conflict between binocular disparity and monocular cue; that is, disparity signaled a slant of  $\pm 30^\circ$  whereas texture signaled a  $0^\circ$  slant (fronto-parallel plane). Thus, adaptation to stimuli in our study might have involved the disparity recalibration process; therefore, the aftereffects occurred independently of retinal position. On the other hand, there was no conflict between binocular disparity and monocular cue in the stimuli used in the previous studies that demonstrated position-dependent depth aftereffects. In the stimuli used in those studies, both disparity and monocular cues signaled a frontal-parallel plane or the stimuli had quite weak monocular cue (Köhler & Emery, 1947; Mitchell & Baker, 1973). Therefore, adaptation to the stimuli in those studies might not have involved the disparity recalibration process. In the case here, aftereffects might have been mainly mediated by disparity selective neurons in area V1; consequently, the aftereffects were dependent on retinal position.

In summary, we demonstrated that the occurrence of depth aftereffects was not always restricted to the retinal position stimulated during adaptation. This finding suggests that a higher mechanism in which the operation is independent from the stimulated retinal position might be responsible for retinal position-independent slant aftereffects, although further examination will be needed to precisely clarify the mechanism. Our findings, together with other recent studies (Domini et al., 2001; Duke & Wilcox, 2003), provide evidence that higher level adaptation is involved in depth aftereffects.

## Acknowledgements

The authors wish to thank Phillip Duke, Takahiro Kawabe, Hiroyuki Mitsudo, and Hiroshi Ono for reading the earlier version of this manuscript and providing many useful comments and suggestions. We also wish to thank Kazuo Koga for his cooperation in measuring eye movements.

This research was in part supported by JSPS (Japan Society for Promotion of Science) to the first author, and was in part supported by Grant-in-Aid for the 21st Century COE Program and by Grant-in-Aid for International Collaborative Researches from TAO to the third author.

## References

Adams, W. J., Banks, M. S., & van Ee, R. (2001). Adaptation to three-dimensional distortions in human vision. *Nature Neuroscience*, *4*, 1063–1064.

- Balch, W., Milewski, A., & Yonas, A. (1977). Mechanisms underlying the slant aftereffect. *Perception and Psychophysics*, *21*, 581–585.
- Berends, E. M., & Erkelens, C. J. (2001). Adaptation to disparity but not to perceived depth. *Vision Research*, *41*, 883–892.
- Bergman, R., & Gibson, J. J. (1959). The negative after-effect of the perception of a surface slanted in the third dimension. *American Journal of Psychology*, *72*, 364–374.
- Blakemore, C., & Julesz, B. (1971). Stereoscopic depth aftereffect produced without monocular cues. *Science*, *171*, 286–288.
- Boussaoud, D., Desimone, R., & Ungerleider, L. G. (1991). Visual topography of area TEO in the Macaque. *The Journal of Comparative Neurology*, *306*, 554–575.
- Bradshaw, M. F., & Rogers, B. J. (1996). The interaction of binocular disparity and motion parallax in the computation of depth. *Vision Research*, *36*, 3457–3468.
- Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, *18*, 193–222.
- Domini, F., Adams, W., & Banks, M. S. (2001). 3D after-effects are due to shape and not disparity adaptation. *Vision Research*, *41*, 2733–2739.
- Duke, P. A., & Wilcox, L. M. (2003). Adaptation to vertical disparity induced-depth: implications for disparity processing. *Vision Research*, *43*, 135–147.
- Epstein, W., & Morgan-Paap, C. L. (1974). The effect of level of depth processing and degree of informational discrepancy on adaptation to unocular image magnification. *Journal of Experimental Psychology*, *102*, 585–594.
- Graham, M., & Rogers, B. (1982). Simultaneous and successive contrast effects in the perception of depth from motion-parallax and stereoscopic information. *Perception*, *11*, 247–262.
- Howard, I. P., & Rogers, B. J. (2002). *Seeing in depth*, Vol. 2, *Depth perception*. Toronto: I. Porteous.
- Janssen, P., Vogels, R., & Orban, G. A. (2000). Three-dimensional shape coding in inferior temporal cortex. *Neuron*, *27*, 385–397.
- Jackson, G. R., Owsley, C., & McGwin, G. Jr., (1999). Aging and dark adaptation. *Vision Research*, *39*, 3975–3982.
- Köhler, W., & Emery, D. A. (1947). Figural after-effects in the third dimension of visual space. *American Journal of Psychology*, *60*, 159–201.
- Landy, M. S., Malony, L. T., Johnston, E. B., & Young, M. J. (1995). Measurement and modeling of depth cue combination: in defense of weak fusion. *Vision Research*, *35*, 389–412.
- Long, N., & Over, R. (1973). Stereoscopic depth after-effects with random-dot patterns. *Vision Research*, *13*, 1283–1287.
- Mitchell, D. E., & Baker, A. G. (1973). Stereoscopic aftereffects: evidence for disparity-specific neurons in the human visual system. *Vision Research*, *13*, 2273–2288.
- Nguyenkim, J. D., & DeAngelis, G. C. (2003). Disparity-based coding of three-dimensional surface orientation by macaque middle temporal neurons. *Journal of Neuroscience*, *23*, 7117–7128.
- Poom, L., & Börjesson, E. (1999). Perceptual depth synthesis in the visual system as revealed by selective adaptation. *Journal of Experimental Psychology: Human Perception and Performance*, *25*, 504–517.
- Rose, D., & Price, E. (1995). Functional separation of global and local stereopsis investigated by cross-adaptation. *Neuropsychologia*, *33*, 269–274.
- Ryan, C., & Gillam, B. (1993). A proximity-contingent stereoscopic depth aftereffect: evidence for adaptation to disparity gradients. *Perception*, *22*, 403–418.
- Sato, M., & Howard, I. P. (2001). Effects of disparity-perspective cue conflict on depth contrast. *Vision Research*, *41*, 415–426.

- Seyama, J., Takeuchi, T., & Sato, T. (2000). Tilt dependency of slant aftereffect. *Vision Research*, *40*, 349–357.
- Tsutui, K., Sakata, H., Naganuma, T., & Taira, M. (2002). Neural correlates for perception of 3D surface orientation from texture gradient. *Science*, *298*, 409–412.
- Wenderoth, P. (1970). A visual spatial aftereffect of surface slant. *American Journal of Psychology*, *83*, 576–590.
- Wilcox, L. M., & Duke, P. A. (2003). Stereoscopic surface interpolation supports lightness constancy. *Psychological Science*, *14*, 525–530.