

# On-off selectivity and asymmetry in apparent contrast: An adaptation study

**Hiromi Sato**

Department of Psychology, Graduate School of  
Humanities and Sociology, The University of Tokyo,  
Tokyo, Japan



**Isamu Motoyoshi**

Department of Life Sciences, The University of Tokyo,  
Tokyo, Japan



**Takao Sato**

Department of Psychology, Graduate School of  
Humanities and Sociology, The University of Tokyo,  
Tokyo, Japan



**Using textures composed of sparse bright/dark elements that can activate either on or off sensors selectively, Sato, Motoyoshi, and Sato (2012) reported simultaneous contrast-contrast effects tuned for contrast polarity. As with contrast-contrast effects, prolonged viewing of high-contrast stimuli reduces the perceived contrast of a subsequently presented stimulus. The present study examined whether contrast aftereffects are also selective for luminance polarity using texture patterns composed of sparse bright/dark elements. Results revealed that contrast aftereffects are selective for luminance polarity (polarity selectivity) but that adaptation aftereffects occur asymmetrically depending on the polarity of the adapter (polarity asymmetry). Polarity selectivity and asymmetry in adaptation aftereffects are reduced but not completely diminished if adapter and test stimuli are presented to separate eyes (dichoptically). Our results support the idea that suprathreshold contrast perception and its adaptational shifts are jointly determined by responses between monocular and binocular units.**

opposite polarity. Such results depart from previous experiments using dense textures wherein the magnitude of simultaneous contrast-contrast effects was found to depend on contrast energy and to be nonselective for contrast polarity (Solomon, Sperling, & Chubb, 1993). Our results therefore suggest that contrast-contrast effects depend more on spatial interactions between visual channels selective for luminance polarities than previously thought, and that polarity-selective effects are concealed if dense textures are used as stimuli.

The simultaneous contrast-contrast effect mentioned above primarily reveals contrast interactions in the spatial domain. However, another effect known as contrast adaptation (wherein the perceived contrast of a texture is reduced after prolonged viewing of a high contrast texture) reveals contrast interactions in the temporal domain (Blakemore & Campbell, 1969; Graham, 1989; see Webster, 2011, for details on adaptation). These two phenomena, contrast-contrast and contrast adaptation, can be considered as analogous phenomena occurring in different domains (Clifford, 2002; Tolhurst & Barfield, 1978). Given that spatial contrast-contrast exhibits polarity selectivity in sparse displays, it is quite plausible that contrast adaptation would do so in sparse display as well. The main objective of this study was to examine whether contrast adaptation exhibits a polarity selectivity similar to that already observed with low-density (i.e., sparse) spatial contrast-contrast stimuli.

In Experiment 1, we examined the polarity selectivity of perceived contrast aftereffects using sparse texture stimuli. In particular, we investigated whether adapta-

## Introduction

We have already reported that the simultaneous contrast-contrast effect is selective for contrast polarities if the stimulus is composed of a sparse (i.e., low-density) array of texture elements (Sato, Motoyoshi, & Sato, 2012). That is, with such sparse stimuli, the simultaneous contrast-contrast effect is more pronounced if the central texture has the same contrast polarity as the surrounding texture instead of the

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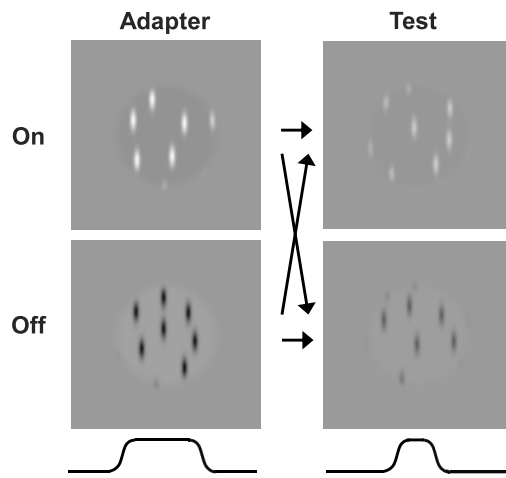


Figure 1. Examples of stimuli used in Experiment 1.

tion-driven shifts in apparent contrast depend on the congruency of luminance polarities between test and adapter. In Experiment 2, we examined the orientation selectivity of polarity dependency using similarly sparse stimuli. Results from our previous experiment on spatial contrast-contrast (Sato et al., 2012) indicated that polarity selectivity is only weakly selective for stimulus orientation. Finally, in Experiment 3, we examined interocular transfers of the aftereffect in an effort to identify the processing level of polarity-selective adaptation.

## Experiment 1

### Methods

#### Observers

Nine naïve observers (AM, AW, LSO, MM, MH, NK, SK, TI, and TS) and one of the authors (HS), all with corrected-to-normal vision, participated in the experiment.

#### Apparatus

Images were generated by using a graphics card (CRS ViSaGe) controlled by a host computer (DELL Precision T1600), and displayed on a 21-inch CRT (MITSUBISHI Diamondtron RD21 or SONY GDM-F500) with a refresh rate of 60 Hz. The luminance of the CRT monitor was carefully calibrated by means of ColorCAL, a high-performance colorimeter (Cambridge Research Systems, Kent, UK). The pixel resolution of the CRT was 1.72 min/pixel at a viewing distance of 1.0 m. The mean luminance of the homogenous field was 53 cd/m<sup>2</sup> for AM, AW, HS, MM, SK, TI, and 30 cd/m<sup>2</sup> for the other observers.

### Stimuli

Stimuli were composed of either one (in the adapting period) or two (in the test period) circular texture patterns of 3.4° diameter (Figure 1). The texture was composed of elongated blobs defined by a two-dimensional Gaussian function with standard deviations of 0.09° (short axis) and 0.29° (long axis). Thus the number of blobs within the circular area was not constant. All elements were vertically oriented, and each element was randomly placed with a minimum center-to-center separation of 0.86°. The elements had either positive (ON) or negative (OFF) contrast polarity, and all elements within a texture pattern had a congruent polarity. The mean luminance of texture pattern was equal to the mean luminance of the background homogenous field. To implement this last requirement, the background luminance of the circular texture region was lowered for stimuli with positive elements and raised for stimuli with negative elements by an appropriate amount. The absolute contrast of the texture was defined as  $|L_{\max} - L_0|/L_0$  when the polarity was positive, and  $|L_{\min} - L_0|/L_0$  when negative, where  $L_0$  is the luminance of background within a texture pattern, and  $L_{\max}$  and  $L_{\min}$  the positive and negative peaks of blob elements respectively.

### Procedure

The effects of adaptation were measured by comparing the perceived contrast of the test stimulus to a matching stimulus presented either to the adapted position or to an equidistant but unadapted position on the other side of fixation. The fixation point was presented at the center of the stimulus field and subtended 0.1° by 0.1°. The distance from the fixation point to the center of the adapting stimulus was 5.7°. The location of the adapter was fixed either on the right or left side of the fixation point for each session and was counterbalanced between sessions.

Prior to each session, observers were adapted to the uniform background for 2 min; then they were adapted to the adapting stimulus, a texture pattern as shown in Figure 1, for 60 s. At the beginning of each trial, the adapting stimulus, a texture pattern as shown in Figure 1, was presented for 6 s at a position to the right or to the left of the fixation point. After 333 ms, this adapting period was followed by a test period that lasted for 1 s.

In the test period, the test and the matching stimulus were presented side by side. The test was presented at the position of the adapter, and the matching stimulus was presented on the other side of the fixation point. The contrast of the adapter was fixed at 1.0. The contrast of the test was either 0.3 or 0.5. The onset and offset of the test and matching stimuli were tapered by a cosine of 666 ms. Test stimuli with contrasts lower than 0.3 were not used since they were often invisible

after adaptation (see Motoyoshi & Hayakawa, 2010). The configuration of elements within the adapting texture was randomly updated every 1000 ms (1 Hz). For five observers (HS, LSO, NK, MH, and TS), we additionally examined a condition in which the adapting texture was updated every 100 ms (10 Hz).

The adapting stimulus had either positive or negative polarity. The polarity of adapter and test were either congruent (congruent condition, ON-ON or OFF-OFF) or incongruent (incongruent condition, ON-OFF or OFF-ON, Figure 1). Thus, there were 16 different conditions (adapter polarity  $\times$  adapter-test polarity congruency  $\times$  test contrast  $\times$  temporal frequency).

Observers viewed the stimuli binocularly and were asked to press one of two buttons to indicate which of two stimuli, either the test or the matching stimulus, appeared to have a higher contrast (2AFC). Observers were instructed not to judge the overall brightness or darkness of the stimulus field but judge the contrast, or the strength, of elements. No feedback was provided.

The matching point between the test and matching stimuli—the point of subjective equality (PSE) for perceived contrast—was measured using a staircase method. The contrast was decreased by a 0.1 log unit when the observer judged that the matching stimulus had a higher contrast than the test, and was increased by a 0.1 log unit when the observer judged the contrast of matching stimulus was lower. The polarity, position (right or left side of the fixation point), and temporal frequency of the adapter were fixed within each session, and the polarity of the adapter was alternated between sessions. Four staircases, each corresponding to a different condition (2 test contrasts  $\times$  2 polarity congruencies), were randomly interleaved within each session. The staircase was terminated when the number of trials in all of the series of staircases exceeded 30. Sessions were repeated several times until at least 100 trials of the data were collected for each condition.

After the experiment, the proportion of “higher contrast” responses were fitted with a logistic function by means of the maximum-likelihood method, and the contrast that yielded 50% probability was taken as the matched contrast, or PSE. The standard error for each PSE was estimated through bootstrapping of 5000 samples.

## Results

Figure 2 shows the obtained PSE values as a function of the physical contrast of the test stimulus. The diagonal dashed line indicates the points where the perceived and physical contrasts are equal. As can be seen from the graph, all observers showed declines in perceived contrast (i.e., contrast aftereffects occurred in all conditions).

The strength of the aftereffect, however, was different between the congruent and incongruent conditions. Aftereffects were larger in the congruent condition (filled symbols) than in the incongruent condition (open symbols). These results indicate that contrast adaptation at suprathreshold levels is selective for contrast polarity (polarity selectivity). To confirm this polarity selectivity, we performed a two-way ANOVA (repeated measures, Table 1) on the obtained matched value (log-scale) from ten observers using adapter/test polarity congruency (same/different) and adapter polarity (ON/OFF) as factors of interest and tested separately for each of four combinations of conditions (2 test contrast  $\times$  2 temporal frequency). The main effects of congruency were significant for all conditions and suggest that contrast adaptation is selective for contrast polarity.

The other prominent result trend is that aftereffects were found to be more profound if the adapter has a negative polarity (OFF) instead of a positive polarity (ON). This polarity asymmetry exists regardless of the adapter/test polarity congruency. Results from the two-way ANOVA above show that adapter polarity was a significant factor except for the 0.5 test contrast  $\times$  10 Hz adapter temporal frequency condition (Table 1). There was a significant interaction between polarity congruency and polarity of adapter only for 0.3 test contrast  $\times$  1 Hz conditions.

## Control experiments

In the above experiment, we equalized the average luminance of the adapters and the tests to that of the background homogenous field in order to minimize the effect of luminance adaptation across stimuli. Because of this manipulation, however, the background luminance within each stimulus varied depending on the polarities and contrasts of texture elements. This may have affected the visual system’s luminance adaptation level and, in turn, it is possible that the difference in the background luminance had some effects on the polarity selectivity and/or asymmetry we found.

To examine this possibility, we conducted an additional experiment in which we examined aftereffects using stimuli with a constant background luminance regardless of the combination of polarity (the mean luminance of each stimuli was not equal in this case). The absolute contrast of the tests was 0.5, and that of the adapters was 1.0. The luminance of the element’s background was kept equal with the homogenous stimulus field (53 cd/m<sup>2</sup>). Results showed the same polarity selectivity and asymmetry as the main experiment albeit a weaker effect for polarity asymmetry. For polarity selectivity, the aftereffects were stronger for same polarity stimuli (PSE 0.23,  $\pm$ 0.01 SEM; six observers) than for opposite polarity stimuli

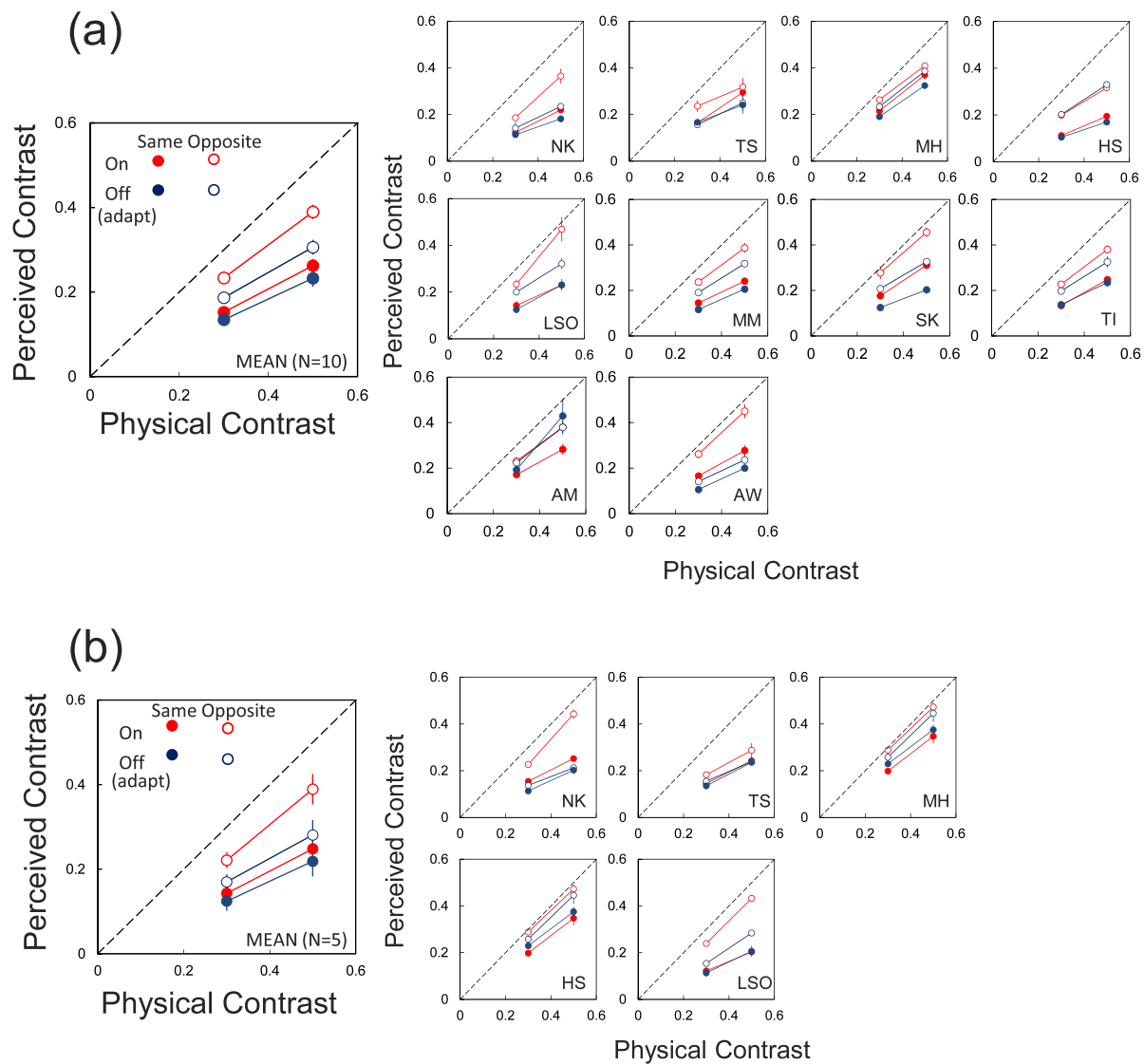


Figure 2. The effects of adaptation on perceived contrast. Matched contrast is plotted as a function of the physical contrast of test stimuli. The dashed line represents the case where matched contrast is equivalent to physical contrast. Filled circles show results for adapters and tests with identical polarities, and open circles show results for adapters and test of opposite polarities. Red circles show results for adapters with positive polarity, and blue circles the results for the adapters with negative polarity. (a) Result for the 1-Hz adapter, and (b) results for the 10-Hz adapter. The left panel shows the average across observers, and the right small panels shows results for individual observers. Error bars represent  $\pm 1$  SEM.

(PSE 0.4,  $\pm 0.40$  SEM). For polarity asymmetry, aftereffects were slightly stronger for the Off adapters (PSE 0.30,  $\pm 0.03$  SEM) than for the On adapters (PSE 0.33,  $\pm 0.03$  SEM). The result of a two-way, log-scaled ANOVA (repeated measure within observer), with the polarity congruency and adapter polarity as factors of interest, showed a significant effect of polarity congruency,  $F(1, 5) = 20.49$ ,  $p < 0.01$ ,  $\eta_p^2 = 0.80$ , power  $(1-\beta) = 0.99$ ; and the polarity of adapter,  $F(1, 5) = 7.66$ ,  $p < 0.05$ ,  $\eta_p^2 = 0.61$ , power  $(1-\beta) = 0.98$ . There was no significant interaction,  $F(1, 5) = 0.01$ ,  $p = 0.94$ ,  $\eta_p^2 = 0.00$ , power  $(1-\beta) = 0.05$ . These results show that variations in background luminance are not the main

cause of polarity selectivity and asymmetry in contrast adaptation.

## Experiment 2: Orientation selectivity

In the second experiment, we examined the orientation selectivity of the polarity-selective mechanism we discovered in Experiment 1. Past studies have reported orientation selectivity in contrast adaptation (Blake-more & Campbell, 1969; Blakemore & Nachmias,

Temporal frequency	Test contrast	Source of variation	Sum of square	Degree of freedom	Mean square	$F$	$\eta_p^2$	Power (1- $\beta$ )	
1 Hz	0.3	Polarity congruency (A)	0.0740	1	0.0740	8.69*	0.49	1.00	
		Polarity of adapter (B)	0.0576	1	0.0576	11.61**	0.56	1.00	
		A $\times$ B interactions	0.0992	1	0.0992	12.00**	0.57	1.00	
		Total	0.5674	39					
	0.5	A	0.2109	1	0.2109	33.54****	0.49	1.00	
		B	0.0616	1	0.0616	8.78*	0.79	1.00	
		A $\times$ B interactions	0.0069	1	0.0069	3.26	0.27	0.86	
		Total	0.5609	39					
	10 Hz	0.3	A	0.1323	1	0.1323	17.67*	0.82	1.00
			B	0.0384	1	0.0384	8.06*	0.67	1.00
A $\times$ B interactions			0.0037	1	0.0037	1.23	0.23	0.71	
Total			0.4086	19					
0.5		A	0.0885	1	0.0885	35.13**	0.90	1.00	
		B	0.0688	1	0.0688	6.58	0.62	0.98	
		A $\times$ B interactions	0.0000	1	0.0000	0.00	0.00	0.05	
		Total	0.3948	19					

Table 1. Two-way ANOVA table. Notes: \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.005$ , \*\*\*\* $p < 0.001$ .

1971), but our previous experiment on spatial contrast-contrast using similar stimuli (Sato et al., 2012) revealed only weak orientation selectivity.

## Methods

The stimuli and procedure remained the same as for Experiment 1 with the exception that, in the present experiment, the orientation of adapting and test/matching stimuli differed by 90°. Nine observers, including one of the authors (HS, MF, MW, RI, RK, MM, SK, TI, AM, and AW), participated in this experiment. Among the nine observers, seven (HS, MF, MW, MM, SK, AM, and AW) were tested with vertical adapters, and two (RI, RK) were tested with horizontal adapters. In the test phase, test and matching stimuli had the same orientation, and the orientation was either identical or orthogonal to that of the adapter. Both identical and orthogonal conditions were conducted for all observers. The mean luminance of the homogenous field was 53 cd/m<sup>2</sup> for HS, MF, MW, MM, SK, AM, and AW, and 30 cd/m<sup>2</sup> for the other observers.

## Results

Figure 3 shows perceived contrast (the point of subjective equality between test and matched contrasts) versus physical contrast as a function of the adapter-test orientation difference. Values larger than 1.0 indicate an increase in perceived contrast whereas values smaller than 1.0 indicate a decrease.

If aftereffects are selective to orientation, we would expect to find little or no aftereffects in cases where adapter-test orientations are orthogonal and similar levels of aftereffect in the two conditions if aftereffects are not selective for orientation at all.

As is clear from Figure 3, the relative perceived contrast after adaptation is smaller than 1.0 in all conditions, thereby indicating that perceived contrast was decreased by adaptation. We also found that aftereffects are more pronounced for identical conditions than for the orthogonal condition regardless of adapter-test polarity congruency. In order to examine the effects of orientation congruency statistically, we performed a three-way ANOVA (repeated log-scaled, within-observer measures) with relative adapter-test orientation (0/90°), polarity congruency between adapter and test (same/opposite), and adapter polarity (ON/OFF) as factors of interest. The analysis revealed significant effects for all three factors: orientation differences,  $F(1, 8) = 19.77$ ,  $p < 0.005$ ,  $\eta_p^2 = 0.71$ , power (1- $\beta$ ) = 1.00; polarity congruency,  $F(1, 8) = 102.68$ ,  $p < 0.0001$ ,  $\eta_p^2 = 0.93$ , power (1- $\beta$ ) = 1.00; and adapter polarity,  $F(1, 8) = 22.53$ ,  $p < 0.005$ ,  $\eta_p^2 = 0.74$ , power (1- $\beta$ ) = 1.00. No interaction was found for any combination of factors. Although these results seem to suggest that aftereffects exhibit orientation selectivity, results from a one sample, two-sided  $t$  test show that, if adapters and tests have the same polarity, the relative perceived contrast after adaptation is significantly different from 1.0 even in the orthogonal condition ( $t$  test in log scale,  $p < 10^{-18}$ ,  $d = 17.569$ , power (1- $\beta$ ) = 1.00. Given the *small*  $p$  value and the huge effect size ( $d = 17.569$ ) in the result of this  $t$  test, it is more natural to conclude that polarity-selective mechanisms contribut-

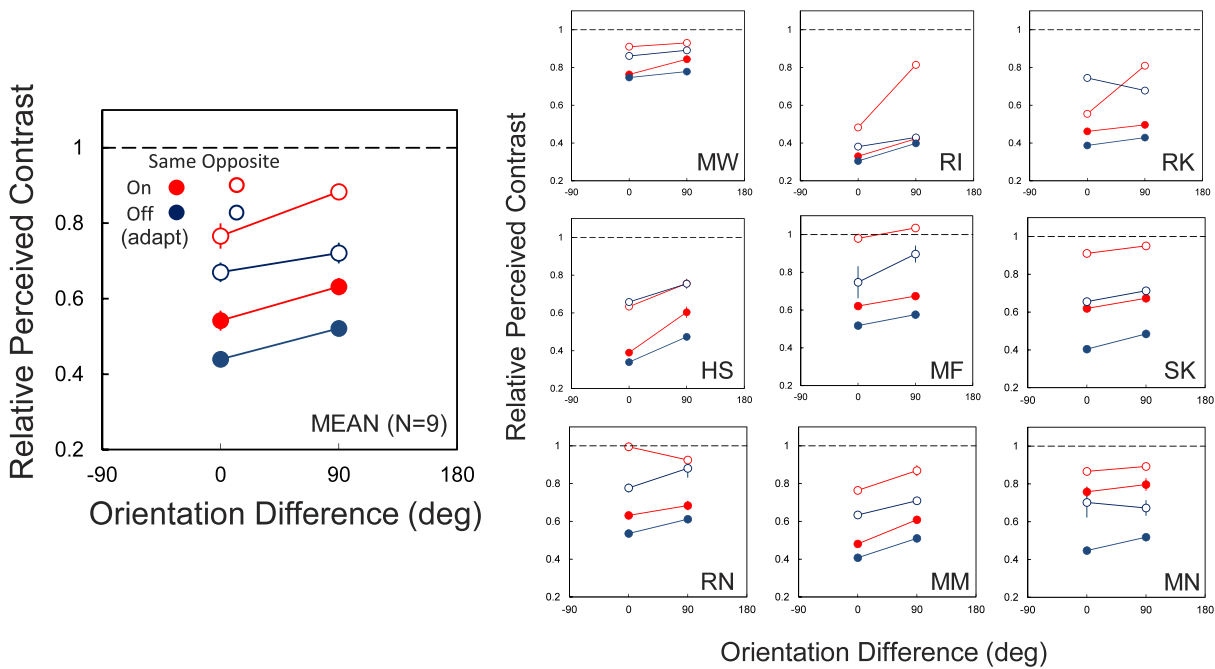


Figure 3. Orientation selectivity. Matched contrast versus physical contrast as a function of adapter-test orientation differences. Values larger than 1.0 indicate an increase in perceived contrast, and values smaller than 1.0 indicate a decrease. The left panel shows the average across observers, and the right small panels shows results for individual observers. Filled circles show the results when the adapter and test have the same polarities, and open circles the results when they have opposite polarities. Red circles show results for a positive adapter, and blue circles the results for the negative adapter. Error bars represent  $\pm 1$  SEM.

ing to contrast aftereffects are not selective for orientation.

### Experiment 3: Interocular transfer

We next wondered if polarity selectivity and polarity asymmetry emerge in the very early stages of visual processing (e.g., in the retina) or in the relatively later processing stages such as visual cortex. To address this question, we examined the interocular transfer of the aftereffect and asked whether properties of the aftereffect remained in spite of the adapter and test being presented to different eyes (Baker & Meese, 2012; Blake, Overton, & Lema-Stern, 1981; Maffei, Fiorentini, & Bisti, 1973; Snowden & Hammett, 1996).

### Methods

The perceived contrast of the test stimuli was measured under monoptic and dichoptic presentations by using stimuli similar to those used in Experiments 1 and 2. The adapting stimuli were presented to one eye, and the test stimuli were presented to the same eye (monoptic condition) or the other eye (dichoptic condition). The adapting and the test stimuli had a

diameter of  $3.4^\circ$ . The separation from the fixation point to the center of each stimulus was  $3.6^\circ$ . The contrast of the adapter was 1.0, and that of the test stimulus was 0.5. Monoptic and dichoptic conditions were randomized within each session, and observers were unaware of which eye the adapter and test were being presented to. With the exception of the aforementioned finer points, the methods remained were the same as in the previous experiments. The data obtained for the left and right eyes were pooled. Four observers including one of the authors (HS, AH, MF, and YM) participated in this experiment.

### Results

Figure 4 shows matched versus physical contrast as a function of the eye condition. Values larger than 1.0 indicate an increase in perceived contrast, and values smaller than 1.0 indicate a decrease. Aftereffects in the monoptic condition duplicate the results obtained in the binocular condition in Experiment 1. In the dichoptic condition, however, the aftereffect is substantially weakened but still remains. As in many previous experiments on the interocular transfer of contrast aftereffects (Bjrkland & Magnussen, 1981; Blake et al., 1981; Selby & Woodhouse, 1980), we

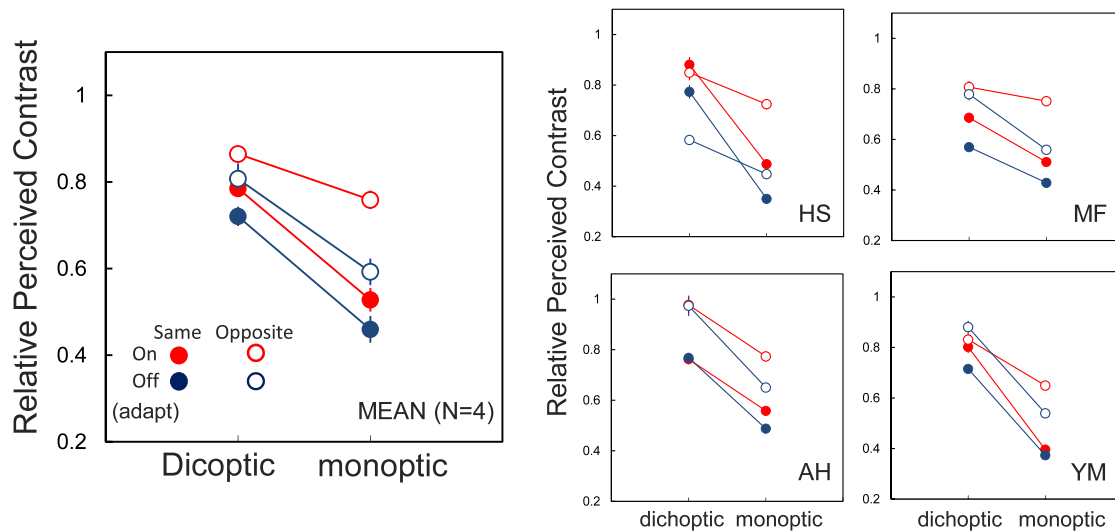


Figure 4. Interocular transfer of contrast aftereffects. Matched contrast versus physical contrast is plotted as a function of eye conditions. The left panel shows the average across observers, and the right small panels shows the results for individual observers. Filled circles show results for adapters and tests with identical polarities, and open circles show results for adapters and test of opposite polarities. Red circles show the results for the positive adapter, and blue circles the results for the negative adapter. Error bars represent  $\pm 1$  SEM.

found large individual differences in the amount of interocular transfer across all conditions.

Figure 5a shows the polarity selectivity of the aftereffect as defined by differences in perceived contrast between same- and opposite-polarity conditions. Values smaller than 1.0 indicate that perceived contrast decreased more if the adapter and test had identical polarities. If polarity selectivity originates completely from binocular mechanisms, then the amount of polarity selectivity in the dichoptic condition would be comparable to that in the monoptic condition. On the other hand, if polarity selectivity originates completely from monocular mechanisms,

then the level of polarity selectivity in the dichoptic condition would be 1.0 in the plot. This plot shows that polarity selectivity was found in both conditions but that the strength of the aftereffect in the dichoptic condition was smaller than in the monoptic condition. The results of a three-way ANOVA (repeated log-scaled measures), with eye condition (monoptic/dichoptic), adapter-test polarity (same/opposite), and adapter polarity (ON/OFF) as the factors of interest show a significant effect of eye condition,  $F(1, 3) = 42.24, p < 0.01, \eta_p^2 = 0.93$ , power  $(1-\beta) = 1.00$ ; and polarity congruency,  $F(1, 3) = 21.54, p < 0.05, \eta_p^2 = 0.88$ , power  $(1-\beta) = 1.00$ . The interaction between eye

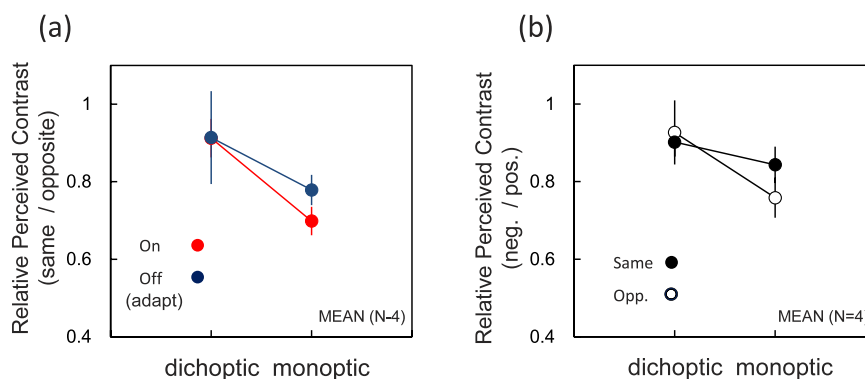


Figure 5. (a) Interocular transfer of polarity selectivity. The abscissa shows eye conditions (dichoptic vs. monoptic), and the ordinate shows the perceived contrast for the same-polarity adapters relative to opposite-polarity adapters. Red circles show results for positive-polarity adapters, and blue circles the results for negative-polarity adapters. (b) Interocular transfer of the polarity asymmetry. The abscissa shows eye condition, and the ordinate shows the perceived contrast for the positive-polarity adapters relative to the negative-polarity adapters. Filled circles show results for adapters and tests with identical polarities, and open circles show results for adapters and test of opposite polarities. Data represent observer averages. Error bars represent  $\pm 1$  SEM.

condition and polarity congruency was not significant. This result indicates the involvement of both monocular and binocular mechanisms in polarity selectivity.

Figure 5b shows the amount of polarity asymmetry as defined by the ratio of perceived contrasts for negative- versus positive-polarity adapters. Values smaller than 1.0 would indicate that perceived contrast decreased more if the adapter had a negative polarity. As in the case of polarity selectivity, the plot shows that the dichoptic condition produces smaller but nonzero polarity selectivity than the monoptic condition. The results from the three-way ANOVA described above show no significant effect of adapter polarity,  $F(1, 3) = 7.44$ ,  $p = 0.07$ ,  $\eta_p^2 = 0.71$ , power  $(1-\beta) = 1.00$ . The interaction between eye condition and adapter polarity was significant. The simple main effect of adapter polarity was significant in the monoptic condition but not in the dichoptic condition. These results are somewhat complicated, but indicate at the very least an involvement of monocular mechanisms in polarity asymmetry.

## Discussion

Results from the first experiment indicate that contrast aftereffects are polarity dependent for sparse textures. That is, larger aftereffects were observed when adapter and test stimuli had identical rather than opposite polarities. This is in accordance with results from our previous experiments on spatial contrast induction (Sato et al., 2012). However, our present results go against the generally accepted notion that such interactions are mediated by early visual stages that encode unsigned contrast, or contrast energy (Cannon & Fullenkamp, 1991, 1993; Foley, 1994; Legge & Foley, 1980; Ohzawa, Sclar, & Freeman, 1985). Thus, the present results on spatial adaptation suggest that channels sensitive to On- or Off-contrast are independently involved in contrast perception. As we mentioned earlier, this study used a sparsely distributed texture pattern whereas most past studies have used texture patterns with higher densities (Solomon, Sperling, & Chubb, 1993). It is plausible, then, that dense patterns tend to stimulate both On- and Off-units whereas sparse patterns stimulate the two types of cells selectively.

There has been an argument that adaptation and simultaneous contrast reflect inhibitory interactions between visual channels across time and space (Clifford, 2002; Tolhurst & Barfield, 1978). In line with this model, the polarity-selective manifestations of contrast perception revealed for adaptation (present study) and simultaneous contrast (Sato et al., 2012) are consistent with the broader notion that the perception of image

contrast largely involves polarity selective channels. However, the present adaptation study also found a polarity asymmetry whereby Off adapters have a greater impact on the perceived contrast of subsequent stimuli. Such an asymmetry was not observed in the simultaneous contrast-contrast (Sato et al., 2012). Although the reasons for this discrepancy remain unclear, the fact that early visual channels are generally more sensitive to Off transients than to On transients (Bowen, Pokorny, & Smith, 1989; Kelly, 1979; Short, 1966; Komban et al., 2011, 2014) hints at a role that transients may play in explaining our adaptation results. Transients would have more impacts on perceived contrast if target onset strictly follows the adapter instead of appearing simultaneously with the surrounding pattern. Such a differential availabilities of transient signals might have produced the on-off asymmetry found in the present adaptation experiments.

Several past studies have shown that some aftereffects such as size aftereffect (De Valois, 1977), shape-frequency after-effect (Gheorghiu & Kingdom, 2006), symmetry after-effect (Gheorghiu, Bell, & Kingdom, 2014), adaptation to temporal sawtooth modulation of luminance (Anstis, 1973; Hanly & Mackay, 1979), and metacontrast masking (Becker & Anstis, 2004) are selective for luminance polarity. While not directly addressing the issue of apparent contrast in supra-threshold stimuli, these studies are largely consistent with the idea that aftereffects in some visual attributes depend on a luminance polarity congruency between test and adapter.

In Experiment 2, it was found that the aftereffects showed little selectivity for orientation. These results also go along with those obtained in our previous experiments on spatial contrast induction (Sato et al., 2012) and support the notion that perceived contrast is largely determined by mechanisms that are not selective for orientation such as those with isotropic receptive fields. This conjecture is also supported by observations that polarity-based texture discrimination does not exhibit orientation selectivity at all (Motoyoshi & Kingdom, 2007).

The aftereffect reported herein shows a partial interocular transfer regardless of the relative adapter-test polarity (Experiment 3). The degree of interocular transfer in our stimuli (~40%) is comparable to that obtained in recent studies measuring interocular transfer of contrast adaptation across a wide range of spatiotemporal frequencies (e.g., Baker & Meese, 2012; Bjrklund & Magnussen, 1981; Blake et al., 1981). Incomplete interocular transfer in polarity-selective and nonselective components suggests that interactions between visual channels mediating perceived contrast reduction occur both in monocular and binocular stages.



There was one peculiar finding in our study. In Experiment 1, the effect of adaptation was larger when the adapter had a negative polarity than when it had a positive polarity, though this polarity asymmetry was reduced in the dichoptic adaptation (Experiment 3). Such results would follow naturally from observations that Off channels exhibit greater gain than On channels; Off-channel dominance has been documented by a number of psychophysical studies wherein human observers are reportedly more sensitive to Off stimuli than to On stimuli (Bowen et al., 1989; Kelly, 1979; Short, 1966). Simple reaction time is also shorter for Off stimuli than for On stimuli (Del Viva, Gori, & Burr, 2006; Komban, Alonso, & Zaidi, 2011; Komban et al., 2014; Kremkow et al., 2014; Del Viva & Gori, 2008), and Off signals contribute to discriminating between textures whose histograms are equated in mean and in variance (Chubb, Econopouly, & Landy, 1994; Chubb, Landy, & Econopouly, 2004). In a study whose results perhaps best matches ours, Chubb and Nam (2000) have shown that Off signals dominate in perceived-contrast discrimination tasks in texture patterns. Physiological studies show that Off units substantially outnumber On units (Ahmad, Klug, Herr, Sterling, & Schein, 2003; Dacey & Petersen, 1992; Jiang, Purushothaman, & Casagrande, 2015) and have greater population response in retina, LGN and V1 (Fiorentini, Baumgartner, Magnussen, Schiller, & Thomas, 1990; Yeh, Xing, & Shapley, 2009; Zemon, Gordon, & Welch, 1988). Ratliff, Borghuis, Kao, Sterling, and Balasubramanian (2010) recently pointed out that such dominance of the Off mechanism is consistent with a processing constraint designed to maximize information availability for natural images. The On/Off asymmetry observed herein also could be accounted for by adaptations to such statistical structure of natural scenes.

*Keywords:* contrast adaptation, luminance polarity, polarity selectivity, polarity asymmetry

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Corresponding author: Hiromi Sato.  
Email: sato@l.u-tokyo.ac.jp.  
Address: Department of Psychology, Graduate School of Humanities and Sociology, The University of Tokyo, Tokyo, Japan.

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