Polarity selectivity of spatial interactions in perceived contrast

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The apparent contrast of a texture is reduced when surrounded by another texture with high contrast. This contrast–contrast phenomenon has been thought to be a result of spatial interactions between visual channels that encode contrast energy. In the present study, we show that contrast–contrast is selective to luminance polarity by using texture patterns composed of sparse elongated blobs. The apparent contrast of a texture of bright (dark) elements was substantially reduced only when it was surrounded by a texture of elements with the same polarity. This polarity specificity was not evident for textures with high element densities, which were similar to those used in previous studies, probably because such stimuli should inevitably activate both on- and off-type sensors. We also found that polarity-selective suppression decreased as the difference in orientation between the center and surround elements increased but remained for orthogonally oriented elements. These results suggest that the contrast–contrast illusion largely depends on spatial interactions between visual channels that are selective to on–off polarity and only weakly selective to orientation.

Keywords: polarity selectivity, spatial interactions, perceived contrast


Introduction

The contrast of a texture pattern appears to be lower when it is surrounded by another texture with a high contrast (Cannon & Fullenkamp, 1993; Chubb, Sperling, & Solomon, 1989; Petrov, Carandini, & McKee, 2005; Sagi & Hochstein, 1985; Solomon, Sperling, & Chubb, 1993; Xing & Heeger, 2000). This contrast–contrast (2nd-order) effect is distinguished from the classical brightness–contrast (1st-order) effect (Chubb et al., 1989; McCourt, 2005) and has been extensively investigated to elucidate visual mechanisms underlying the perception of image contrast. Past psychophysical studies have shown that the contrast–contrast effect depends on differences in orientation and spatial frequency between the central and surround regions (Cannon & Fullenkamp, 1993; Chubb et al., 1989; Solomon et al., 1993; Xing & Heeger, 2000) and is observed even when the surround region is not consciously perceived (Cai, Zhou, & Chen, 2008; Motoyoshi & Hayakawa, 2010). These findings are consistent with the notion that the contrast–contrast effect is primarily caused by inhibitory lateral interactions between low-level visual channels, i.e., spatial filters (Cannon & Fullenkamp, 1993, 1996; Chubb et al., 1989; Ejima & Takahashi, 1985; Sagi & Hochstein, 1985). Similar mechanisms have been assumed to underlie spatial interactions observed in detection threshold (Polat & Sagi, 1993; Zenger & Sagi, 1996), perceived orientation (Blakemore, Carpenter, & Georgeson, 1970), and perceived spatial frequency (Klein, Stromeyer, & Ganz, 1974). The potential neural correlates of such interactions have been reported for neurons in V1 (Blakemore & Tobin, 1972; Knierim & van Essen, 1992; Zipser, Lamme, & Schiller, 1996), although their anatomical origin is still controversial (Webb, Dhruv, Solomon, Tailby, & Lennie, 2005). From a computational viewpoint, these second-order spatial interactions are considered as useful for efficient image coding (Schwartz & Simoncelli, 2001), texture segmentation (Graham, 2011), and motion detection (Chubb & Sperling, 1988). Many studies point out that they also play a role for estimation of distal object properties such as reflectance and transparency (Adelson, 1999; Dakin & Mareschal, 2000; Lotto & Purves, 2001; Schofield, Hesse, & Rock, 2006; Solomon & Mareschal, unpublished draft; Spehar, Arend, & Gilchrist, 1995).

Current models of the contrast–contrast phenomenon generally assume that contrast perception is mediated by...
mechanisms that encode absolute (unsigned) contrast, i.e., contrast energy (Cannon & Fullenkamp, 1996; Solomon et al., 1993). This is a natural assumption since observers are asked to judge unsigned contrast, but it is not necessarily true. It has been known that the mammalian visual system has not only neural units sensitive to unsigned contrast but also to either positive (on) or negative (off) contrast (Fiorentini, Baumgartner, Magnussen, Schiller, & Thomas, 1990; Jung, 1973; Schiller, Sandell, & Maunsell, 1986). These on- and off-type sensors have classically been thought to underlie the perception of brightness and darkness (Anstis, 1979; Blakeslee & McCourt, 2004; Jung, 1973). However, they could be involved in various judgments on spatial patterns. Psychophysical evidence shows that visual aftereffects in contrast detection threshold (Hanly & MacKay, 1979), perceived spatial frequency (De Valois, 1977), and contour shape (Gheorghiu & Kingdom, 2007) substantially depend on the combination of luminance polarity between the adapting and test stimuli. Similar segregation between on- and off-contrast information has been shown for texture discrimination (Chubb, Econopouly, & Landy, 1994; Chubb, Landy, & Econopouly, 2004; Malik & Perona, 1990; Motoyoshi & Kingdom, 2007). However, such a separation has not been found between stimuli of sine and anti-sine phases (Huang, Kingdom, & Hess, 2006; Malik & Perona, 1990). These findings lead us to the notion that the appearance of a textural pattern depends at least partially on separate representations of on and off contrasts.

Is the contrast–contrast effect selective for luminance polarity? Solomon et al. (1993) addressed this question by using center–surround texture patterns composed of dense bright or dark dots. They found that perceived contrast in the central region is reduced by the surrounding region regardless of whether it is composed of bright dots or dark dots, indicating no polarity selectivity. These results seem to be consistent with a model of contrast–contrast effect as being mediated by units encoding contrast energy. There is, however, a possibility that, as we shall explain later in more detail, such dense textures activate both on- and off-type sensors regardless of the elements’ luminance polarity.

In the present study, we show that when texture is composed of sparse elements that selectively stimulate on or off units, contrast–contrast shows a clear selectivity to luminance contrast polarity. Figure 1 shows examples of stimuli. In Experiment 1, we demonstrated that the central texture appears to have lower contrast when it is surrounded by a texture of the same polarity than when surrounded by that of the opposite polarity. In Experiment 2, we found that this polarity selectivity of contrast suppression diminished for textures made of dense elements, as previously reported by Solomon et al. (1993). In Experiment 3, we also showed that this polarity-selective suppression is slightly weakened as the difference in elements’ orientation was increased between the center and the surround. On the basis of these results, we suggest that the contrast–contrast effect involves polarity-selective, and partially orientation-selective, visual mechanisms.

Experiment 1

Methods
Observers
Four naive participants (AY, KA, MH, and RY) and one of the authors (HS), with corrected-to-normal vision, participated in the experiment.

Apparatus
Images were generated by a graphics card (CRS Visage) and displayed on a 21-inch CRT (Eizo Flex Scan T962, SONY GDM F520R only for AY) with a refresh rate of 160 Hz. 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 63 cd/m² for AY and 54 cd/m² for the other observers.

Stimuli
The stimuli for this experiment consisted of standard and test stimuli. The standard stimulus was a circular
texture region surrounded by an annular inducing texture as shown in Figure 1. The diameter of the central field was 2.9 deg and that of the surround field was 8.6 deg. The central field of the standard stimulus alone was presented separately and used as a test stimulus. The two stimuli were presented side by side on both sides of a black fixation dot (0.1 × 0.1 deg) at the center of a homogenous stimulus field (22.9 × 17.2 deg). The separation from the fixation dot to the center of each stimulus was 5.7 deg.

The texture was composed of elongated blobs defined by a two-dimensional Gaussian function with standard deviations of 0.07 deg (short axis) and 0.23 deg (long axis). All elements were vertically oriented. Each element was randomly placed with a minimum center-to-center separation of 0.64 deg. The elements within each field had the same value of either positive or negative contrast polarity. The combinations of polarities between the center and surround were varied as shown in Figures 1a–1d. The absolute contrast of the texture field was defined as $|L_{\text{max}} - L_{0}|/L_{0}$ when the polarity was positive and $|L_{\text{min}} - L_{0}|/L_{0}$ when negative, where $L_{0}$ is the luminance of elements’ background and $L_{\text{max}}$ and $L_{\text{min}}$ are the positive and negative peaks of blob elements, respectively. The contrast of the surround field was 1.0, and that of central field was varied between 0.125, 0.25, and 0.5.

The mean luminance of each texture field—the test stimulus and the center and surround of the standard stimulus—was equated to the mean luminance of the background homogenous field. Therefore, the background luminance ($L_{0}$) within each texture field varied depending on the contrast polarity of texture elements. Because of this luminance difference, there was a luminance (first-order) edge between the center and surround of the standard stimulus. The magnitude of luminance difference and the clarity of the contour vary depending on the contrast polarity. To control the clarity of the border between the center and surround fields, we added a black circular contour (0.06 deg in width) having the same diameter as the central field to mask this luminance contour. This circle also helped the observers to segregate the center from the surround and prevented unnecessary crowding of elements. It was quite possible that addition of this black contour affect the result. We checked this by a pilot experiment. The results are basically the same between the conditions with or without the black contour, but it was so much easier for observers to judge when there was a black circle.

**Procedure**

We measured the matching point between the standard and test stimuli, i.e., the point of subjective equality (PSE) for perceived contrast, by using a staircase method. Observers binocularly viewed the stimuli and fixated on the fixation dot through each trial. At the beginning of each trial, the fixation marker and the circles alone for both stimuli were presented. Both standard and test stimuli appeared 500 ms later and were presented for 500 ms. The circles stayed on for 500 ms after standard and test stimuli disappeared. Early onset of the circle for 500 ms was useful for getting observers attend to the image regions to be compared.

The observers were asked to press one of two buttons to indicate which of the standard or test stimulus appeared to have a higher contrast (2AFC). They were instructed (1) not to judge the overall brightness or darkness of the stimuli but the contrast, or the strength, of elements and (2) to concentrate on the central regions designated by the black circles. No feedback was given.

The contrast of the test stimulus was varied in accordance with the staircase method. It was decreased by 0.1 log unit when the observer indicated that the test stimulus had a higher contrast than the standard and was increased by 0.1 log unit when the observer indicated that it had a lower contrast. Within a single session, 12 staircases each corresponding to a different condition were randomly interleaved. In each session, the staircase terminated when the number of trials in all of the staircases exceeded 30. Session was repeated several times, until at least 120 trials of the data (83 for AY) were collected for each condition. The proportion 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 2a shows the matched contrast of test stimulus as a function of the physical contrast of the standard stimulus. The left panel shows the average of all observers, and the right small panels show the results for each observer. (The average was calculated on the log coordinate.) Red circles represent the results when the center had positive polarity, and blue circles represent the results when the polarity of the center was negative. Filled circles show the results when the center and surround had the same polarities, and open circles show the results when they had opposite polarities. The perceived contrast is lower than actual when the center had the same contrast polarity as the surround (filled circles). However, when the center had an opposite polarity to the surround, the matched contrast appears almost equal to the physical contrast (open circles), indicating no suppression.

Figure 2b shows the matched contrast relative to the physical contrast. The same center–surround polarity (filled symbols) produced strong suppression at all contrast levels of the center. On the other hand, the opposite center–surround polarity (open symbols) produced little, if any, suppression except for the lowest contrast of the center. These results suggest that contrast–contrast is selective to luminance contrast polarity for a wide range of suprathreshold contrast levels.
Control experiments

In the above experiment, we equalized the mean luminance between the center and surround regions to minimize the effect of spatial luminance contrast across regions. Because of this control, however, the background luminance within each region varied depending on the contrast of texture elements, and this variation produced sharp luminance edges at the boundary between two regions. Although these edges were made invisible by presenting circular contours, it is possible that the difference in the background luminance still had some other effects.

We thus examined the contrast suppression using stimuli with a constant background luminance regardless of the combination of polarity. In this additional experiment, the absolute contrast of the center was 0.5, and that of the surround was 1.0. The luminance of the element’s background was kept equal with the homogenous stimulus field (54 cd/m²). We found essentially the same results as

Figure 2. (a) Polarity selectivity of spatial contrast suppression. The matched contrast is plotted as a function of the physical contrast of the standard stimuli. The dashed line denotes the matched contrast equivalent to physical contrast. Filled circles show the results when the center and surround have the same polarities, and open circles show the results when they have opposite polarities. Red circles show results for a positive center, and blue circles show the results for the negative center. The left panel shows the average across observers and the right small panels show the results for individual observers. Error bars represent ±1 SE. (b) The matched contrast relative to the physical contrast. Values larger than 1.0 indicate facilitation, and values smaller than 1.0 indicate suppression.
for the main experiment. The suppression was observed only for the same polarity stimulus (PSE 0.38, ±0.04 SEM; 4 observers) but not at all for the opposite polarity stimulus (PSE 0.51, ±0.02 SEM). In the other additional experiment, we also used textures consisting of isotropic Difference-of-Gaussian (DoG) patterns with standard deviations of 0.07 deg (center Gaussian) and 0.18 deg (surround Gaussian). The absolute contrast of the center was 0.3, and that of the surround was 1.0. We found again that suppression occurred only with the same polarity stimulus (PSE 0.22, ±0.02 SEM; 4 observers) and not with the opposite polarity stimulus (PSE 0.30, ±0.02 SEM). These results indicate that the effect of luminance difference produced by equalization was not the main source of contrast suppression found in the main experiment. In addition, the results with circular texture elements (DoG patterns) indicate that the polarity selectivity does not depend on whether textures consist of oriented or circular elements.

**Experiment 2**

The results of Experiment 1 showed a polarity selectivity for contrast suppression. As previously mentioned, these results are not consistent with those of Solomon et al. (1993). The disagreement could be caused by the difference in the stimulus. While we used sparse textures, Solomon et al. used dense textures. We thus examined the effect of density by systematically manipulating spatial separation between texture elements.

**Methods**

The stimulus was a center–surround texture field as used in Experiment 1. In order to control the element density, we varied the minimum separation between elements for 0.29, 0.36, 0.50, and 0.64 deg (Figure 3). The contrast of the central field was 0.5, and that of the surround was 1.0. Four observers (HS, KA, MH, and RY) participated in the experiment. The mean luminance of the homogenous field was 54 cd/m² for all observers. The mean luminance was equalized between the center and surround regions. The methods are the same except for these points.

**Results**

Figure 4 shows matched contrast relative to physical contrast as a function of density. When texture had relatively high density (inter-element separations of 0.29 and 0.36 deg), perceived contrast was suppressed regardless of the combination of polarities. When the center had relatively low density (0.50 and 0.64 deg), however, suppression occurred only when the center and surround had the same polarities. We further examined the effect by using a dense texture (inter-element separation of 0.29 deg) with relatively low contrast (center and surround

![Figure 3. Examples of stimuli used in Experiment 2. The center-to-center separation between adjacent elements was 0.29, 0.36, 0.50, and 0.64 deg from the left, respectively. The absolute contrast of the center was 0.5, and that of the surround was 1.0 under all conditions. The mean luminance was equalized between the center and surround regions.](https://jov.arvojournals.org/pdfaccess.ashx?url=data/journals/jov/932802/)
contrasts were 0.125 and 0.25) and obtained essentially the same results (PSE 0.09, $\pm$0.01 SEM for same polarity; PSE 0.09, $\pm$0.01 SEM for opposite polarity; 2 observers). Therefore, the lack of polarity selectivity at high density observed in the main experiment is not due to the high contrast used there.

Spatial suppression seems to be polarity selective for textures of sparse elements but not for textures of dense elements. The results indicate that lack of polarity selectivity in the contrast–contrast reported in the previous study (Solomon et al., 1993) is mainly caused by the use of high-density textures. In addition, we found in our pilot observations that the suppression is substantially weakened when the center and surround had different element sizes or densities. This implies a selectivity for spatial frequency and/or texture density of the polarity-dependent suppression. Therefore, the lack of polarity selectivity at high density observed in the main experiment is not due to the high contrast used there.

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### Experiment 3

The results of the above experiments show that contrast suppression is specific to luminance polarity, and this polarity selectivity is not evident for textures with high element densities. It is known that contrast suppression depends on the difference in orientation between center and surround elements (Petrov et al., 2005; Solomon et al., 1993; Xing & Heeger, 2000). However, it is still not clear how orientation dependency relates to polarity selectivity. Solomon et al. (1993) examined both orientation and polarity dependency, but their stimuli were composed of high-density elements. Hence, it remains possible that orientation dependency is peculiar to dense stimuli.

Thus, in this experiment, we examined whether contrast suppression with sparse stimuli is also orientation selective.

## Methods

The stimulus was a texture composed of oriented blobs as used in the previous experiments. The orientation of elements in the center was always vertical, while the orientation of surround was tilted clockwise or counterclockwise by 0, 30, 60, or 90 deg (Figure 5). The contrast of the central field was 0.5, that of the surround was 1.0, and the inter-element separation between elements was 0.64 or 0.36 deg. Three observers (HS, KA, and MH) participated in the experiment. The mean luminance of the homogenous field was 54 cd/m$^2$ for all observers. Mean luminance was equalized between the center and surround regions. The methods except for these points were the same as in Experiment 1. The data for bilaterally symmetric conditions (e.g., 30 deg and $-30$ deg) were pooled in the analysis.

## Results

Figure 6a shows the matched contrast relative to the physical contrast as a function of the orientation difference, as obtained for low-density textures. When the center had the same polarity as the surround, the suppression slightly decreased as the orientation difference increased. The suppression occurred even with orthogonally oriented elements. As we fitted a Gaussian function in the orientation domain to the power spectrum of a texture with sparse elements (at the peak spatial frequency), the estimated standard deviation of a Gaussian was $\sim$20 deg. It is thus unlikely that the suppression at the orthogonal condition ($>$4 sigma distant) was caused by the overlap in the orientation energy of elements. On the other hand, for the condition that the center had an opposite polarity to the surround, little or no suppression was observed over all orientation differences. Figure 6b shows the results for
high-density texture. The suppression occurred regardless of the center–surround polarity combinations and slightly decreased as the center–surround orientation difference increased.

**Discussion**

The present study shows that spatial interactions in the contrast–contrast effect depend on the congruency of luminance polarity between the center and surround texture regions. The perceived contrast of the central texture was markedly reduced (up to 30–40%) by a surrounding texture with the same luminance polarity but not at all by a texture with the opposite polarity. The results support the idea that contrast–contrast is largely mediated by independent spatial interactions between visual units sensitive to on- and off-type contrast rather than interactions between units sensitive to unsigned contrast.

The present results are apparently inconsistent with a previous study that showed no polarity selectivity of spatial interactions. However, the results of Experiment 2 clearly show that this discrepancy is caused by a difference in the density of texture elements. Polarity selectivity was evident for textures with sparse elements but absent for textures with dense elements. This is a natural consequence of the spatial response profile of on- and off-type visual units, which are commonly modeled as band-pass spatial filters followed by half-wave rectification and threshold. Suppose there is a texture pattern composed of bright elements on a dark background. When the elements are sparsely placed in the texture, the filtered outputs of on units would be large enough to exceed the threshold level, but those of off units would not. As a result, this texture selectively activates on units only. On the other hand, when the elements are densely placed, the filtered outputs of off units to the background in between the bright elements can also exceed the threshold. As a result, a high-density texture inevitably activates both on and off units. This would be one of the main reasons for why we and Solomon et al. (1993) did not find polarity selectivity for high-density textures.

A clear polarity selectivity in the contrast–contrast (2nd-order) effect may be considered as a class of brightness/darkness (1st-order) contrast between the elements. That is, the apparent brightness of each element in the center is reduced by high luminance incremental elements in the surround, it would cause a reduction in apparent contrast. Likewise, if the high luminance incremental surround blobs reduce the brightness of the decremental luminance test field elements, this would cause an increase in apparent contrast (or at least would not produce a contrast reduction). The lack of polarity selectivity at high density may reflect the difficulty of segregating elements from the background and represent a shift from first-order to second-order induction (see McCourt, 2005). However, it should be noted that this interpretation hypothesizes the existence of an additional process that segregates elements from background. Therefore, we believe that the present results can be explained more parsimoniously by assuming interactions between on- and off-type spatial filters.

We also found that the suppression effect is selective, though weakly, for orientation as well as for contrast polarity. Similar weak orientation tunings have also been reported for gratings and for line textures (Cannon & Fullenkamp, 1993; Solomon et al., 1993; Xing & Heeger, 2000). Notably, the significant suppression remained when elements in the center had an orientation orthogonal to...
those in the surround. This seems to indicate the involvement of spatial suppression of both orientation-selective and non-selective (isotropic) units. The critical role of polarity-selective isotropic units has also been proposed for texture discrimination (Motoyoshi & Kingdom, 2007; Sharan, Adelson, Motoyoshi, & Nishida, 2007). This idea is consistent, at least partially, with the recent physiological findings that there are two types in surround suppressions of V1 neural activities, one based on interactions between orientation-tuned cortical neurons and the other based on inhibitory inputs from LGN neurons with broader orientation tunings that operate when the center and surround have the same contrast polarity (Soodak, Shapley, & Kaplan, 1987; Webb et al., 2005). The other possible neural substrate for the non-orientation-selective component is intrinsic interactions among cells in CO blobs of V1 (e.g., Ts’o & Gilbert, 1988).

**Conclusion**

The present study showed that the contrast–contrast illusion is selective for luminance polarity except for textures with very high density. The results indicate separate contributions of on/off responses for the perception of image contrast.

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