Flashed stimulation produces strong simultaneous brightness and color contrast

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Simultaneous brightness contrast and simultaneous color contrast are classical illusions that demonstrate how our perception can be altered by spatial context; a central gray region appears to have brightness and color that are complementary to those of a surrounding region. Previous studies have suggested the involvement of a sluggish process in these illusions. On the other hand, a different, fast mechanism has recently been postulated to operate in simultaneous contrast when the stimulus is presented only briefly. Here, we show that in briefly flashed stimuli, not only the simultaneous brightness contrast but also the simultaneous color contrast is perceived with greatly enhanced illusion strength. In simultaneous brightness contrast, inserting a spatial gap between the center and surround weakened the illusion only when the stimulus was flashed. In simultaneous color contrast, the gap weakened the illusion irrespective of stimulus duration. Both brightness contrast and color contrast effects steeply decayed with duration. The present study suggests the existence of a fast-responding process for estimating brightness/color primarily based on local difference in luminance/color along the edge between the center and surround. We argue that the sluggishness of simultaneous contrast demonstrated by previous studies originated from a sluggish process after local and fast spatial interactions.

Keywords: simultaneous brightness contrast, simultaneous color contrast, psychophysics

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Introduction

Brightness and color of one region can be affected by spatial context. Typically, a gray stimulus placed on a bright background appears darker than the same gray stimulus placed on a dark background (e.g., Heinemann, 1955). This phenomenon, called simultaneous brightness contrast, clearly shows the importance of the surrounding luminance in brightness perception. Color perception is also affected by the color of background (simultaneous color contrast). When placed on a colored background, the hue of a color stimulus is shifted toward the complementary color of the background.

The spatial properties of these illusions have been studied widely. In comparison, studies on their temporal properties, although of equal importance, are rare. One of the most influential studies examined center–surround interactions of brightness and color (De Valois, Webster, De Valois, & Lingelbach, 1986). In this study, the central test area was physically stable, whereas the luminance/color of the surrounding area was temporally modulated. The illusory modulation of the brightness/color of the test stimulus decreased with surround modulation frequency and disappeared at approximately 2.5 Hz. This was much lower than the critical flicker frequency of luminance or of color, suggesting that simultaneous contrast involves a slow process. However, several methodological issues should be noted with regard to this study. For example, subjects were instructed to ignore subjective flickers in the test pattern, especially those occurring along the border under high frequency conditions; this may have artificially decreased the cut-off frequency. Rossi and Paradiso (1996) conducted similar experiments and reached the conclusion that because the cut-off frequency of the brightness contrast depended on stimulus size, the sluggishness of the illusion likely stemmed from a slow filling-in process to spread brightness signals from the edges to the inner area.

On the other hand, more recently, simultaneous brightness contrast at a shorter time scale has been reported. Blakeslee and McCourt (2008) demonstrated that brightness contrast was not gradual, as expected from the filling-in theory, but was almost instantaneous, as predicted by their brightness perception model—the oriented difference-of-Gaussian (ODOG) model (Blakeslee & McCourt, 1999)—which consisted of several spatial filters with different spatial properties. Also, Robinson and de Sa (2008) reported that a surrounding

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stimulus of very short duration is sufficient to induce brightness contrast. The brightness change in gray central bars by brighter/darker surrounding bars was seen at surround durations as short as 58 ms and was strongest at this duration. Other illusions such as the Craik–O'Brien–Cornsweet (COC) illusion (Wachtler & Wehrhahn, 1997), tilt contrast, and tilt aftereffect with flashed tests (Wenderoth & Johnstone, 1988; Wenderoth & van der Zwan, 1989; Westheimer, 1990; Wolfe, 1984) have been found to show similar duration-dependent properties. These fast-occurring illusions have one thing in common: They are all driven by a difference between adjacent areas on a local scale.

Thus, current knowledge of simultaneous contrast indicates both slow and fast processes as underlying mechanisms. To obtain a better view of the possible mechanisms, it is important to determine the tuning functions of the fast-occurring illusions. To this end, we conducted a series of experiments to reveal the spatial and temporal properties of simultaneous brightness/color contrast. In Experiment 1, we examined differences in the spatial properties of simultaneous brightness contrast between a brief presentation and a long presentation. After we confirmed that the enhancement of illusion strength in a brief presentation was seen not only in brightness contrast but also in color contrast (Experiment 2), we examined the spatial properties of enhanced color contrast (Experiment 3). We also investigated the temporal properties of color contrast (Experiment 4) and brightness contrast (Experiment 5) on a finer time scale by examining illusion strength as a function of stimulus duration.

Experiment 1

In this experiment, we examined whether spatial adjacency between center and surround is critical in the enhancement of simultaneous brightness contrast at short durations. Because a typical effective stimulus for simultaneous contrast is composed of a central stimulus embedded within a uniform surround without a gap, lateral inhibition is often claimed as a neuronal account for simultaneous contrast. This may not be wholly correct. Short-range effects are not necessarily sufficient to generate a perceptually uniform contrast effect across the enclosed area (Gerrits & Vendrik, 1970); the maximal distance at which the luminance of a remote stimulus can induce brightness contrast is approximately 10° (Yund & Arrington, 1975), which is too far to be explained by lateral inhibition among individual cells at early levels. Nonetheless, local contrast information at the edges of an area is known to determine the strength of conventional simultaneous contrast. Thus, irrespective of the actual underlying neural mechanism, it is meaningful to ask whether local interaction acts differently at different durations.

To address this issue, we inserted a spatial gap between the test stimulus and the surround stimulus in a concentric pattern and manipulated the gap width. If the illusion were purely brought about by local factors that exist along the border, separating the two areas with the gap would critically influence the illusion strength. If, on the other hand, local interaction made a relatively minor contribution, the gap width would have no or little effect on the illusion.

Methods

Subjects

Seven subjects, including one of the authors (SK), participated. All had normal or corrected-to-normal vision.

Apparatus

Stimuli were presented on a CRT display (Mitsubishi Diamondtron M, 22", 33.3° × 25°, refresh rate 100 Hz [Mitsubishi Electric, Tokyo, Japan]) under computer (Apple PowerMac G5 [Apple Inc., Cupertino, CA]) control. Experiments were run in a dark room. Each subject's head was stabilized using a chin rest to maintain a viewing distance of 68.7 cm (binocular viewing).

Stimuli

All stimuli were generated using the MATLAB (The MathWorks, Natick, MA) programming environment with Psychtoolbox (Brainard, 1997; Pelli, 1997) routines. The test stimulus whose brightness was to be measured was a gray disk (radius: 0.5°) with the luminance fixed at 33 cd/m^2 (mean luminance). The comparison stimulus was a gray disk of the same size as the test stimulus, with the luminance adjustable to 0–66 cd/m^2. The distance between the test and comparison stimuli (center to center) was 16.5°. The two disks were presented side by side. The test stimulus was centered at a larger annulus, namely the surround stimulus, of various luminance levels. The outer radius of the surround stimulus was 8.25°. The color of the surround stimulus was occupied by either a uniform gray color of one of the four luminance values, 0 (black), 13 (dark gray), 53 (light gray), and 66 cd/m^2 (white), or by random noise (mean luminance was 33 cd/m^2). The stimulus duration was one display frame ($<$10 ms) or 500 ms. The test and surround regions were changed to uniform mean-luminance gray at the stimulus offset. Therefore, the region of the test disk was physically unchanged at the mean luminance whether the stimulus was on or off, and it was only demarcated by the appearance of surround

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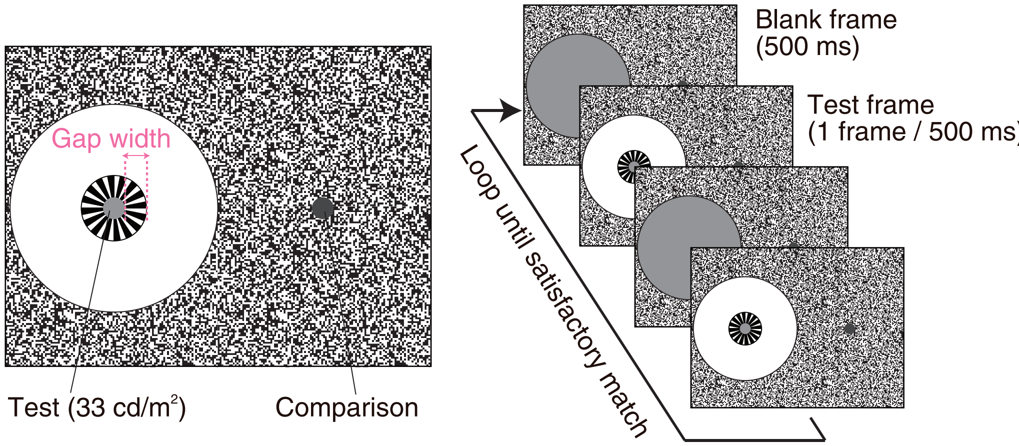

Figure 1. Spatial and temporal configuration of the stimuli used in Experiment 1.

stimuli. Around the test disk, a wheel-like ring consisting of 32 dark and light radial stripes was added as the gap. The mean luminance of the gap was equal to the luminance of the test disk so that the gap itself would induce no overall brightness change in the test disk. The gap was presented together with the surround stimulus. There were three gap conditions: no gap (gap width 0°), narrow gap (0.25°), and wide gap (1°). Random noise (50% black and 50% white) occupied the area outside the stimulus regions (Figure 1).

Procedure

The brightness of the test stimulus was measured using the matching method. Subjects observed the stimuli binocularly and were instructed to move their gaze freely to compare the two disks in terms of brightness. Subjects were asked to adjust the luminance of the comparison stimulus by pressing buttons to match the brightness of the test stimulus. The surround and the gap (except for the no-gap condition) stimuli were repeatedly presented with 500-ms blank intervals until the subject made a satisfactory match. The comparison stimulus was always present during a trial. When the subject indicated that adjustment was complete by pressing the button, random noise filled the whole screen for 3 s to avoid any effect carried over, followed by the next trial. The 10-ms condition and the 500-ms condition were run in separate sessions. The three gap conditions were run in a pseudorandom order within a session. The test stimulus appeared to the left or right of the comparison stimulus (fixed within a session). Each subject made 12 matches per condition.

Results and discussion

We expressed the brightness change in the test stimulus in terms of percent change in the luminance of the matched comparison compared with the luminance of the test stimulus. Therefore, negative and positive values indicated that the test stimulus was matched to a comparison stimulus of lower and higher luminance, respectively. A value of zero indicated that the subject made a veridical match.

Figure 2 shows the average brightness change under each condition. Under almost all conditions, except for the noise-surround condition (baseline control), simultaneous brightness contrast occurred—that is, the test disk appeared darker when the luminance of the surround was greater than that of the test, and the test disk appeared brighter when the luminance of the surround was lower than that of the test disk. Furthermore, the overall strength of the illusion was greater under the 10-ms condition than under the 500-ms condition.

We performed a two-way ANOVA (duration × gap; $\alpha = .05$) on the change in test brightness under each surround condition (excluding the noise-surround condition) independently. A significant main effect of duration was observed for three surround conditions, i.e., light gray: $F(1, 6) = 8.02$, $p = 0.03$; dark gray: $F(1, 6) = 41.67$, $p = 0.0007$; and black: $F(1, 6) = 8.26$, $p = 0.03$. A significant main effect of gap was observed for all surround conditions, white: $F(2, 12) = 10.63$, $p = 0.002$; light gray: $F(2, 12) = 8.94$, $p = 0.004$; dark gray: $F(2, 12) = 4.26$, $p = 0.04$; and black: $F(2, 12) = 24.24$, $p = 6 \times 10^{-5}$. Our question in this experiment was whether the gap had a different effect on illusion strength depending on duration; therefore, the most important outcome was the interaction term. A significant interaction was found for three conditions, white: $F(2, 12) = 24.13$, $p = 6 \times 10^{-5}$; light gray: $F(2, 12) = 47.18$, $p = 2 \times 10^{-6}$; dark gray: $F(2, 12) = 19.56$, $p = 0.0002$), and the remaining condition was marginally significant, black: $F(2, 12) = 3.85$, $p = 0.05$. The test for the simple main effect of gap size revealed no difference among the three gap conditions under the 500-ms condition,

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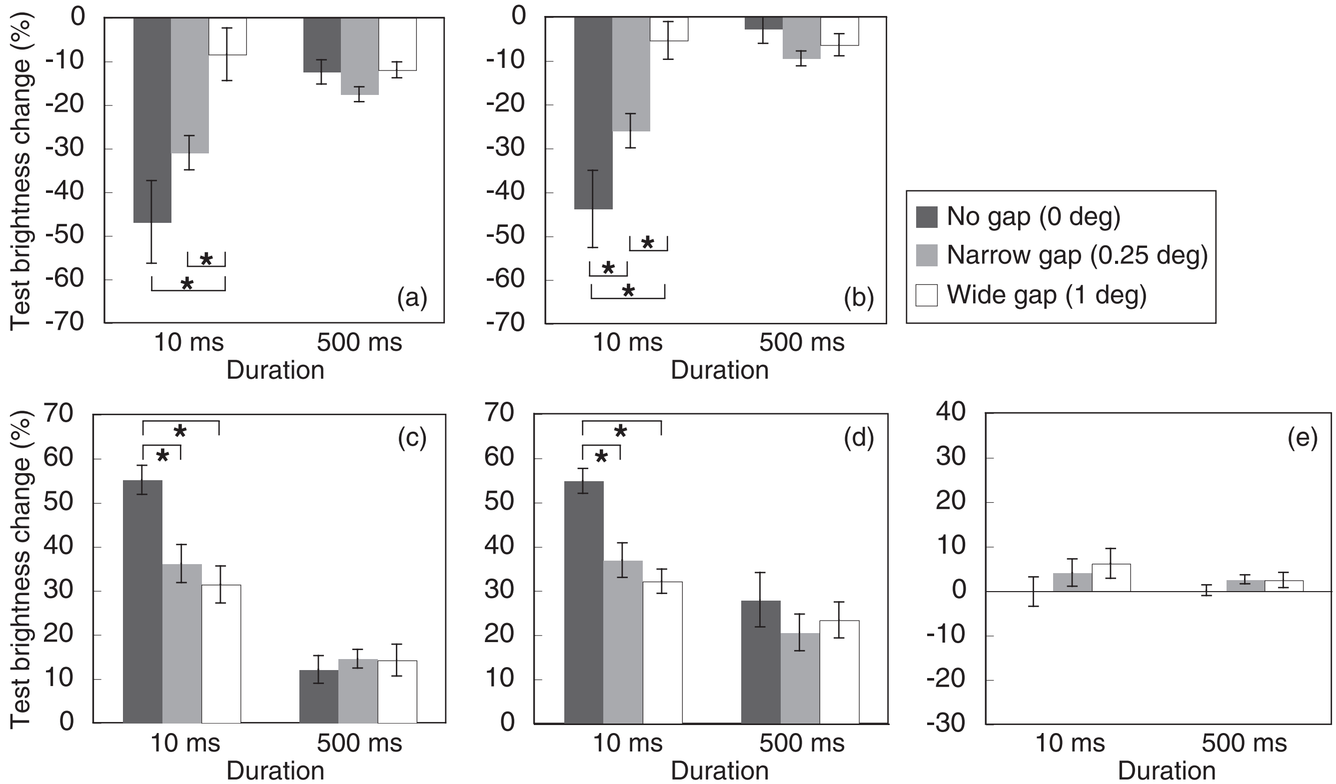

Figure 2. Results of Experiment 1. Averaged ($N = 7$) change in test stimulus brightness is plotted under different surround conditions in separate panels: (a) white (66 cd/m^2), (b) light gray (53 cd/m^2), (c) dark gray (13 cd/m^2), (d) black (0 cd/m^2), and (e) noise (mean luminance 33 cd/m^2). Error bars indicate ± 1 *SE*.

but 9 of 12 possible pairs exhibited significant differences under the 10-ms condition (indicated by the asterisks in Figure 2).

Thus, in the absence of a gap between the test and surround (dark gray bars in Figure 2), the illusion was significantly greater under the 10-ms condition than under the 500-ms condition for all four surround conditions. This result is consistent with the results obtained previously by Robinson and de Sa (2008). Together with their results, our findings thus challenge the conclusion that simultaneous brightness contrast is "slow" in the sense that it requires long exposure of the stimulus.

The gap width affected the illusion strength differently depending on stimulus duration. Under the 10-ms condition, under which the test stimulus lasted only for one display frame, the illusion diminished with increasing gap width. Without a gap, the illusion was much stronger than under the 500-ms condition, but as the gap became wider, the illusion became drastically weaker, even as weak as that under the 500-ms condition in some cases. On the other hand, under the 500-ms condition, the illusion was insensitive to gap width.

These results suggest that the underlying mechanisms generating brightness contrast are different depending on stimulus duration. When the duration is very short, the visual system determines the brightness of a given area primarily based on very local edge-contrast information and produces a powerful illusion. When the duration is long enough, another mechanism that is capable of contrasting the luminance levels over at least 1°of distance is activated. The latter system is less affected by spatial gap. This is probably because cues other than the local luminance difference between adjacent regions are available to the system, such as other luminance edges located farther away and the highest/lowest luminance value. Such cues are known to affect brightness/lightness perception in some situations (Adelson, 2000; Shapley & Reid, 1985; review Gilchrist et al., 1999). We thus argue that the powerful illusion seen in the brief stimulus is the consequence of a fast, built-in calculation of brightness, which is not perfect but good enough to fulfill the demand to see any brightness, and that a slower mechanism uses various cues to estimate brightness that is more consistent with the current scene at the expense of processing time. We will return to this point in the General discussion section.

Experiment 2

In this experiment, we examined whether similar enhancement occurs in color contrast as in brightness

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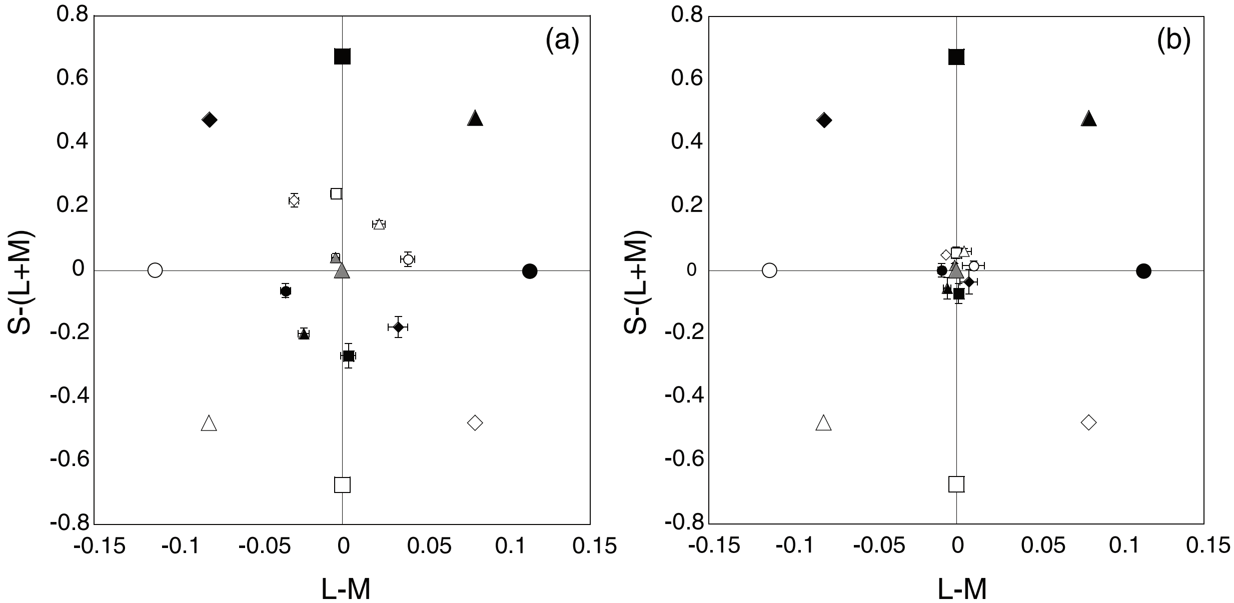

Figure 3. Results of Experiment 2. Averaged ($N = 4$) colors of the matched comparison disk under (a) the 10-ms condition and (b) the 500-ms condition are plotted on the equiluminant plane. Nine larger symbols represent the different surround colors (including the luminance noise condition, indicated by the large gray triangle at the origin). Smaller symbols represent the subjects' matches when the surround had the color indicated by the corresponding symbol. Error bars indicate ± 1 *SE*.

contrast. In De Valois et al.'s (1986) study, similar cut-off temporal frequencies were found for both achromatic and chromatic stimuli with a temporally modulated surround. On the other hand, Robinson and de Sa (2008), who reported that brief exposure was sufficient to induce simultaneous contrast, examined only brightness contrast and not color contrast. Thus, we were interested in whether similar results would be obtained from a chromatic version of our preceding experiment.

Methods

Subjects

Four subjects, including one of the authors (SK), with normal or corrected-to-normal vision participated. All subjects had normal color vision as tested with the Ishihara plates.

Stimuli

The apparatus and stimuli were identical to those used in Experiment 1 except as follows. All colors used in Experiment 2 were on the equiluminant plane passing through the center in the Derrington–Krauskopf–Lennie (DKL) color space (Derrington, Krauskopf, & Lennie, 1984). Eight uniform colors were used for surround colors: two along the $L - M$ axis (red and green), two along the $S - (L + M)$ axis (purple and lime), and the four intermediate colors. The color gamut was hardware dependent. We adjusted the luminance of these eight colors for each subject beforehand to set them as equiluminant to the achromatic gray at the center of the color space using heterochromatic flicker photometry. As in Experiment 1, luminance binary noise texture was also used as one of the surround color conditions. The test disk was identical to that used in Experiment 1, except that a thin (7.5 min) dark contour was added along the border. This contour was added to increase the visibility of the test stimulus and was presented with the surround (not visible during blank intervals). The surround's outer radius was 10°, and a fixation point was provided at the center of the display.

Procedure

The procedure was identical to that of Experiment 1 except for the following. Each session started with a 3 min adaptation to the mean luminance (uniform achromatic gray). Subjects were asked to adjust the hue and saturation of the comparison disk so that its color appeared the same as that of the test stimulus. The color of the comparison disk was adjustable two-dimensionally on the equiluminant plane by button pressing.

Results and discussion

The average color of the matched comparison was plotted on the equiluminant plane, and Figure 3a and b shows the results under the 10-ms and 500-ms

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conditions, respectively. The origin is the achromatic gray used for the test stimulus, and the eight outermost color points indicate the colors used for the surround stimulus. Each point with an error bar indicates the matched color under the condition in which the outermost color indicated by the same symbol was used as the surround color. We confirmed that under each condition, the color of the matched comparison was in the direction of the complementary color with respect to the surround color. Greater separation from the origin indicates stronger color contrast. We also confirmed that the random-noise surround (baseline control) introduced no color change in the test disk.

Simultaneous color contrast was greatly enhanced under the 10-ms condition compared with the 500-ms condition, and this enhancement was almost equally powerful for all the surround colors tested. To assess the strength of the enhancement of the illusion, we performed a two-way ANOVA on the distance between the origin and each point. A significant main effect of test duration, $F(1, 3) = 93.66$, $p = 0.002$, was found, but no main effect of surround color, $F(7, 21) = 0.97$, $p = 0.48$, or duration–color interaction, $F(7, 21 = 1.86$, $p = 0.13$, was found.

The results of Experiment 2 indicate that the enhancement of simultaneous contrast seen in the brightness domain (Experiment 1) also exists in the color domain. The similarity of the results suggests that similar mechanisms underlie both forms of simultaneous contrast.

Experiment 3

In Experiment 1, we found a gap effect; under the 10-ms condition, the strength of the illusion decreased as the gap size increased, whereas under the 500-ms condition, the illusion seemed to be immune to the spatial gap. In Experiment 3, we tested whether a similar effect exists for simultaneous color contrast.

Methods

Subjects

Three subjects, including one of the authors (SK), participated. All had normal or corrected-to-normal vision.

Stimuli

The apparatus and stimuli were identical to those used in Experiment 2, except that we added the textured gap used in Experiment 1. There were three gap-size conditions: no gap (0°), narrow gap (0.25°), and wide gap (1°). Four of the eight previously used colors along the cardinal axes were used for the surround color: purple, lime, red, and green.

Procedure

The procedure was identical to that in Experiment 2 except that subjects could only adjust the saturation of the comparison disk. Adjustment was made along the line on the equiluminant plane connecting the achromatic gray point and the color that each subject had matched to the color perceived in the central test region under the 10-ms condition with the same surround color and without a spatial gap. Hence, the hue of the matched comparison was always constant, and only the saturation was varied. All surround colors and gap conditions were presented in a pseudorandom order within a session. A total of 24 matches were made per condition.

Results and discussion

The matched comparison colors are shown in Figure 4. The vertical axis indicates the color coordinate of the comparison disk along one of the cardinal axes on which the surround color was located. Negative values in Figure 4a and c and positive values in Figure 4b and d correspond to the direction of simultaneous color contrast. As can be clearly seen, simultaneous color contrast was found in all cases, at least under the condition without a gap.

Unlike in Experiment 1, here we found that the gap affected the illusion similarly regardless of the duration condition. Under the 10-ms condition, as in Experiment 1, increasing the gap width reduced the magnitude of the illusion. Under the 500-ms condition, the gap similarly reduced the magnitude of the illusion, as shown by a two-way ANOVA. A significant main effect of gap was found under all surround-color conditions, purple: $F(2, 4) = 55.70$, $p = 0.001$; lime: $F(2, 4) = 12.06$, $p = 0.02$; red: $F(2, 4) = 9.69$, $p = 0.03$; and green: $F(2, 4) = 36.40$, $p = 0.003$, but a significant interaction was found under only one color condition, green: $F(2, 4) = 19.73$, $p = 0.01$. A significant main effect of duration was found for purple and lime, purple: $F(1, 2) = 23.58$, $p = 0.04$; lime: $F(1, 2) = 162.84$, $p = 0.0001$, and a marginally significant main effect was found for red and green, red: $F(1, 2) = 17.61$, $p = 0.05$ and green: $F(1, 2) = 13.57$, $p = 0.07$.

In both Experiment 1 and Experiment 3, we used the same black-and-white patterned gap to separate the test and the surround. We found no systematic difference in the pattern of results when we used the patterned gap with chromatic variation (e.g., a green-and-red gap when the surround was green). (Data not shown.)

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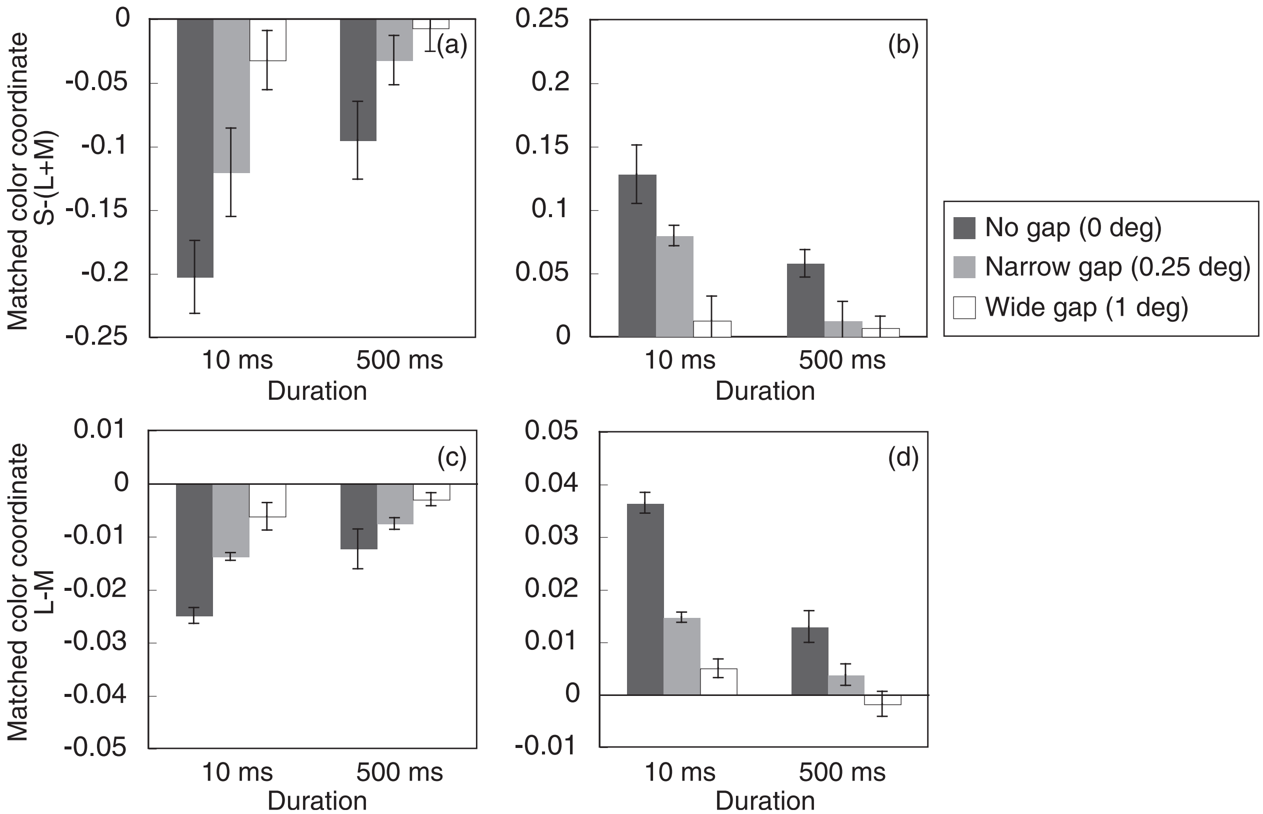

Figure 4. Results of Experiment 3. Averaged ($N = 3$) colors of the matched comparison disk are plotted in separate panels for the different surround colors: (a) purple, (b) lime, (c) red, and (d) green. Error bars indicate ± 1 *SE*.

The data for the 10-ms condition, which show the reduction in the illusion with increasing gap size, indicated an important role for local interactions between test and surround stimuli. Together with those from Experiment 1, these results suggest that the change in both brightness perception and color perception induced by a flashed stimulus is primarily driven by local information along the border. Contrary to the results of Experiment 1, in Experiment 3, the illusion became weaker with increasing gap size under the 500-ms condition as well as under the 10-ms condition. This suggests that unlike in the brightness case, the color seen over longer duration also primarily depended on local information.

Experiment 4

Experiments 2 and 3 demonstrated that simultaneous color contrast was enhanced when the surround stimulus was briefly flashed. To further investigate the temporal properties of the illusion, in this experiment we systematically varied stimulus duration.

Methods

Subjects

Six subjects, including one of the authors (SK), with normal or corrected-to-normal vision participated. All subjects had normal color vision as tested with the Ishihara plates. Two of the subjects had participated in Experiment 2.

Stimuli

The apparatus and stimuli were identical to those in Experiment 2, but as in Experiment 3, four colors along the cardinal axes were used as the surround colors. The duration of the stimulus was varied from one display frame to 640 ms (1, 2, 4, 8, 16, 32, and 64 frames).

Procedure

The procedure was identical to that of Experiment 3.

Results and discussion

Representative data for one naïve subject are shown in Figure 5. The data for the remaining subjects are

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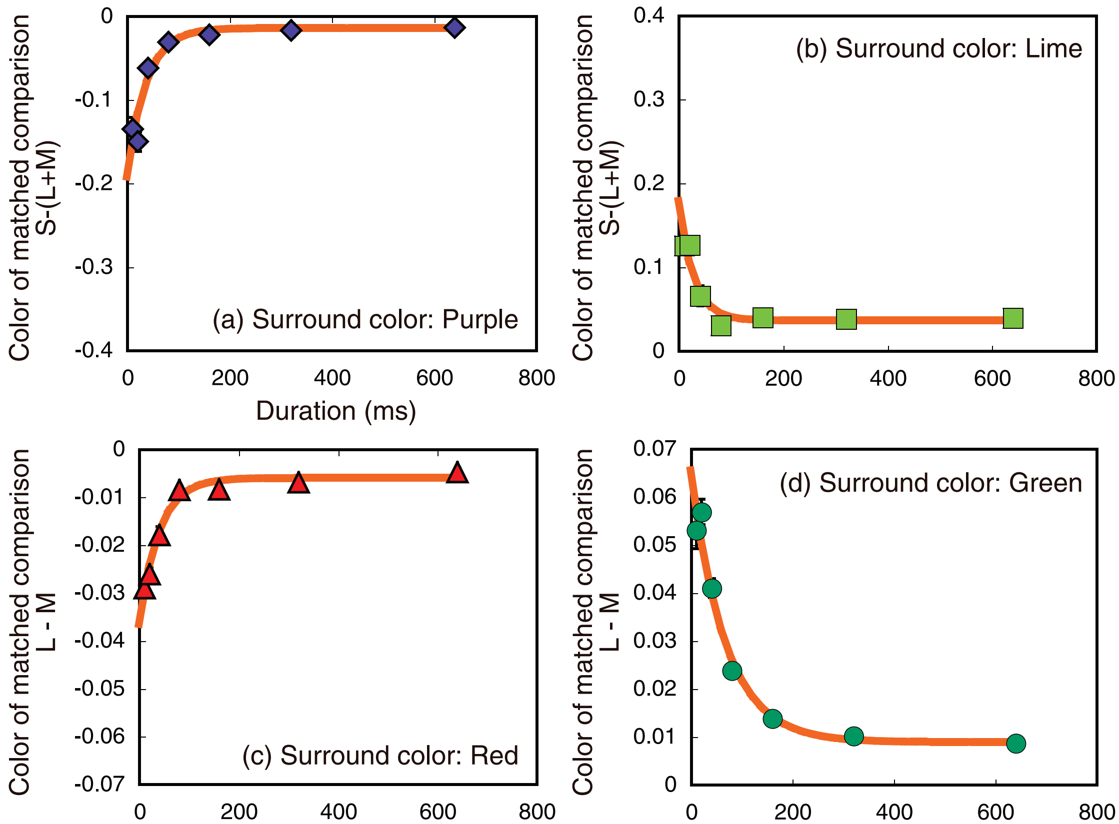

Figure 5. Results of Experiment 4. The color of the matched comparison is plotted against duration. Separate panels correspond to the four surround colors: (a) purple, (b) lime, (c) red, and (d) green. Data for a representative naïve subject (SO) are shown. Each point is the average of 24 matches. Orange curves indicate best-fit models. Error bars indicate ±1 *SE* (most are shorter than the height of the symbol and are thus invisible).

shown in Figure 6. Each point is the average color of the matched comparison at the respective duration. The convention of the vertical axes is identical to that in Figure 4.

Of the six subjects, the illusion strength in all but one showed similar time dependences. The color contrast effect was strongest at the shortest duration, and the illusion strength sharply diminished exponentially with increasing duration. Interestingly, the shapes of the curves were similar among the four different surround-color conditions.

Data of matched colors were fitted with the exponential decay function, designated as

$$f(t) = K\exp(-t/\tau) + C, \tag{1}$$

where t is duration (ms), and other symbols are free parameters.

The mean τ for each condition is shown in Table 1. A two-way ANOVA revealed that τ was not significantly different among the four surround colors, $F(3, 9) = 1.65$, $p = 0.25$. Two subjects were excluded from this statistical analysis because of missing data. One of them (YY) exhibited stronger simultaneous contrast at almost every duration than did most of the other subjects, and virtually no enhancement of the illusion was observed in the flashed stimuli. We believe that the poor fit of this subject's data can be explained by a ceiling effect. The other excluded subject (MS) tended to exhibit a stronger illusion at shorter durations, but the peak under one surround condition occurred at the second shortest rather than at the shortest duration (see Figure 6b).

The results of Experiment 4 demonstrated that the enhanced color contrast rapidly diminished with duration and leveled off at approximately 100 ms, suggesting that the enhancement is a very unusual case that only happens when the duration is extremely brief. In other words, the mechanism responsible for the enhanced illusion seen in the flashed stimuli is narrowly tuned to brief presentation of the stimuli. Whether this is also true for brightness contrast was examined in the next experiment.

Experiment 5

Is rapid decay of the illusion strength as a function of duration also found in brightness contrast? If it is, how rapid is it? To answer these questions, we conducted an equivalent experiment for simultaneous brightness contrast.

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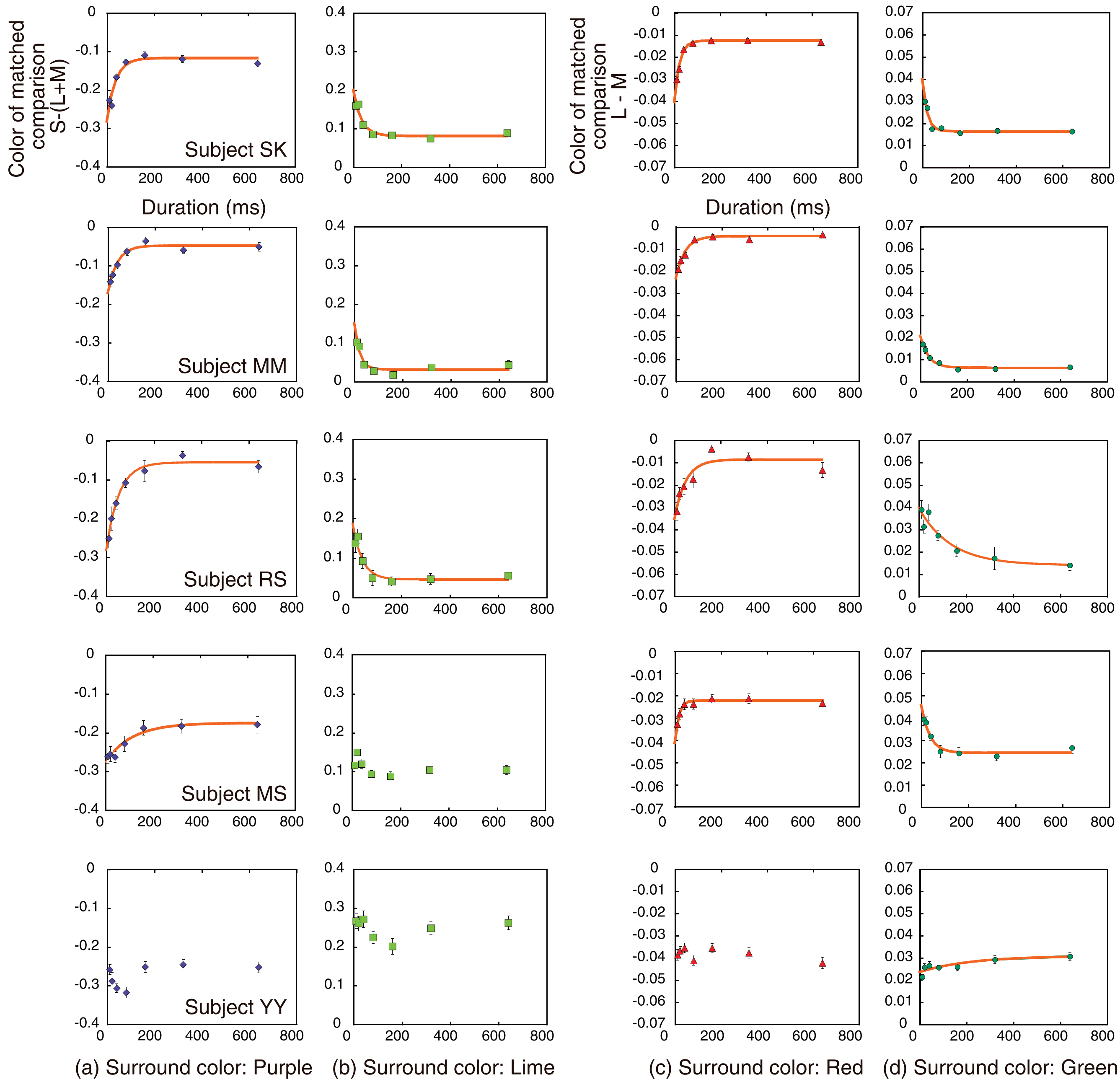

Figure 6. Results of Experiment 4 for the remaining five subjects. Each row shows the data for one subject, and each column shows the results for one surround condition. Conventions are identical to those in Figure 5.

Methods

Subjects

Seven subjects, including one of the authors (SK), with normal or corrected-to-normal vision participated. All subjects had normal color vision as tested with the Ishihara plates. Three of the subjects had participated in Experiment 4.

Stimuli

The apparatus and stimuli were identical to those in Experiment 1, except that as in Experiment 4, the stimulus varied in duration from one display frame to 640 ms (1, 2, 4, 8, 16, 32, and 64 frames).

Procedure

The procedure was identical to that of Experiment 4.

Results and discussion

Representative data for one naïve subject are shown in Figure 7. The data for the remaining subjects are

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	Surround color			
Subject	Purple	Lime	Red	Green
SK	36.74	33.5	22.92	20.36
SO	37.54	28.72	40.36	68.23
MM	39.61	22.39	39.86	35.00
RS	52.88	38.54	48.57	136.12
MS	112.39	—	16.87	36.21
YY	—	—	—	220.00*

Table 1. Time constants (ms) for the four surround colors estimated from the results of Experiment 4. Data for four of the six subjects resulted in good fit ($R^2 > 0.7$, $p < 0.05$) for all conditions. *Notes*: *YY's data in the green surround condition gave a good fit, but the polarity of the curve was opposite to those of the other subjects. The illusion in this case was stronger at longer durations.

shown in Figure 8. Under all conditions, the strong illusion seen at the shortest duration decayed exponentially as the duration increased. As in Experiment 4, the curves for the different surround conditions showed similar shapes.

The brightness matching data were fitted with Equation 1. The time constant τ for each condition is shown in Table 2.

Three subjects participated in both Experiments 4 and 5. For these subjects, the τs for color contrast were consistently smaller than those for brightness contrast. Comparing the mean τs between the two experiments, the difference was 55.92 ms on average, $t(2) = 11.75$, $p = 0.01$ (Figure 9).

Other than the difference between color and brightness, Experiments 4 and 5 had some minor differences in stimuli and procedure, such as the radius of the surround area (5° in Experiment 4 and 8.25° in Experiment 5), the viewing condition (with the fixation point in Experiment 4; free viewing in Experiment 5), and the thin contour along the border between the test and the comparison stimuli (presented only in Experiment 4). It is possible that these minor differences were responsible for the quantitative difference in results between the two experiments. Therefore, we replicated Experiment 5 using one of the authors (SK) and a naïve subject (SO) and employing a modified stimulus configuration (including the smaller surround area,

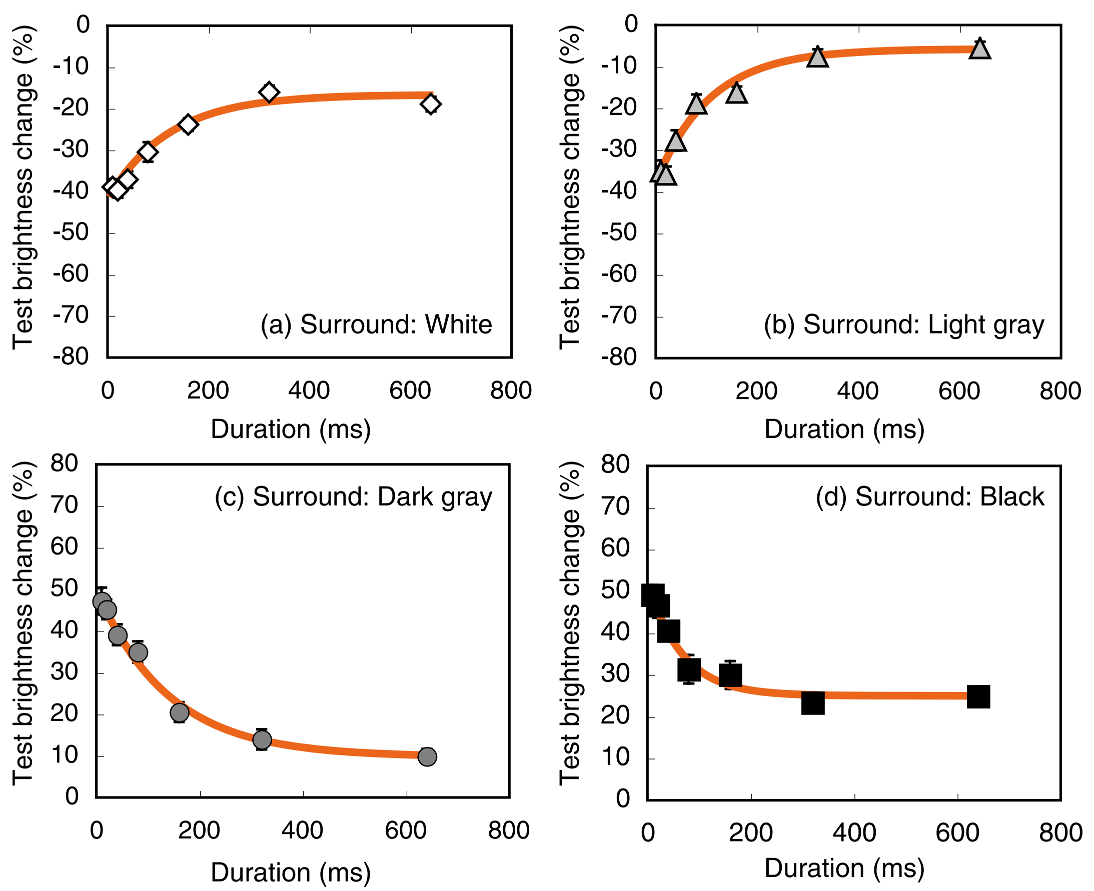

Figure 7. Results of Experiment 5. Change in brightness of the test stimulus is plotted against duration. Separate panels correspond to the four surround colors: (a) white, (b) light gray, (c) dark gray, and (d) black. Data for a representative naïve subject (SO) are shown. Conventions are identical to those in Figure 5.

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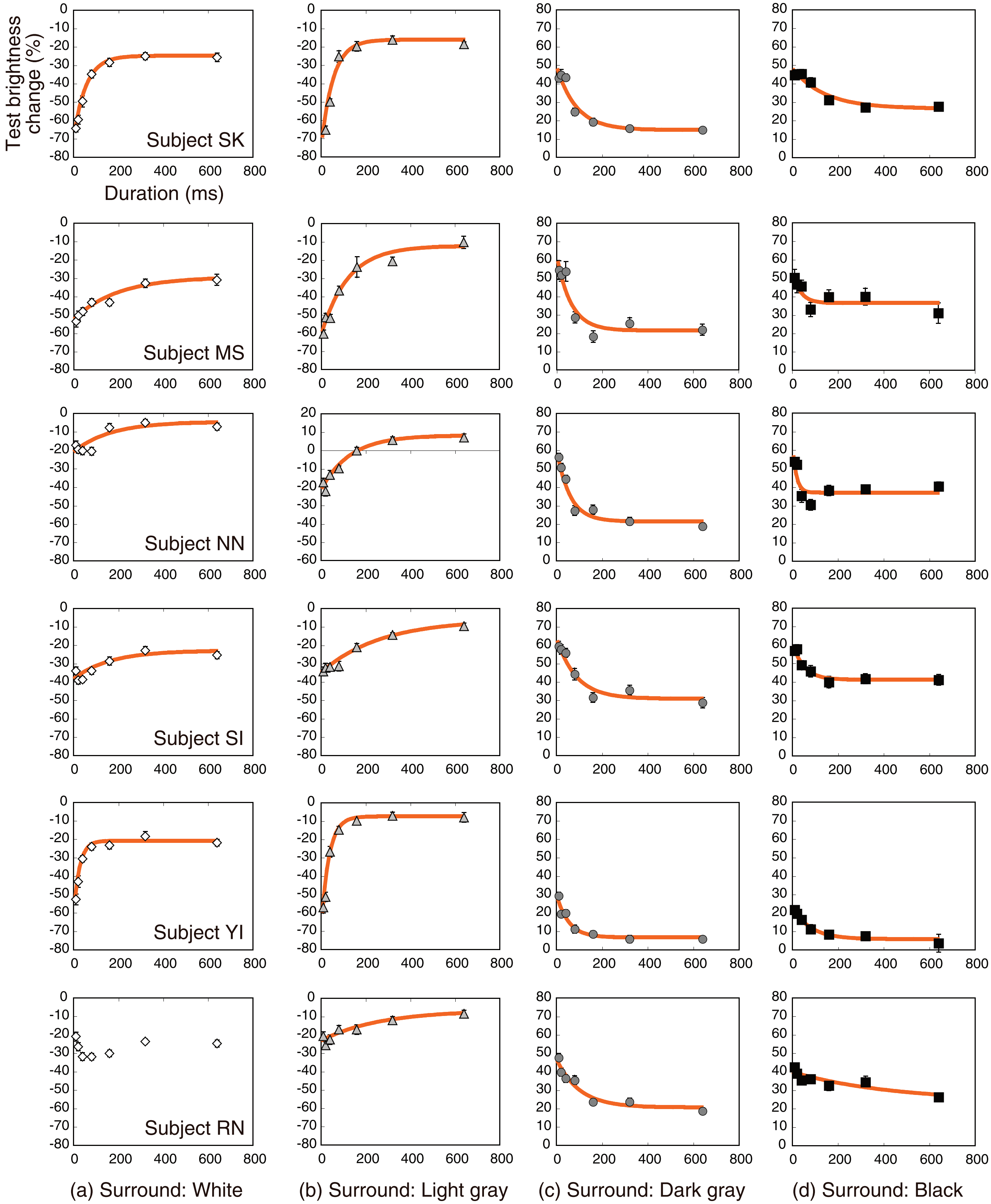

Figure 8. Results of Experiment 5. Data for the remaining six subjects. Each row shows the data for one subject, and each column shows the results for one surround condition. See Figure 7 for other details.

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	Surround color			
Subject	White	Light gray	Dark gray	Black
SK	54.90	53.37	85.71	141.34
SO	119.88	107.32	139.07	66.13
MS	195.69	119.55	62.53	34.54
NN	164.80	128.87	57.27	16.52
SI	161.95	263.69	86.52	49.70
YI	26.27	34.87	52.75	78.65
RN	—	262.75	99.05	432.08

Table 2. Time constants (ms) for the four surround brightness conditions estimated from the results of Experiment 5. Data for six of the seven subjects resulted in good fit ($R^2 > 0.7$, $p < 0.05$) for all conditions.

the fixation point, and the contour). The results of this additional experiment confirmed that the above parameters could not account for the >50 ms difference found between results of Experiments 4 and 5 (data not shown).

As can be seen in Tables 1 and 2, there were large individual differences in illusion strength and τ. However, within subjects, we consistently obtained smaller τ values in Experiment 4 than in Experiment 5. In the next section, we consider the possibility that τ is greater for brightness contrast because some additional process operates, and we discuss our theory about this phenomenon.

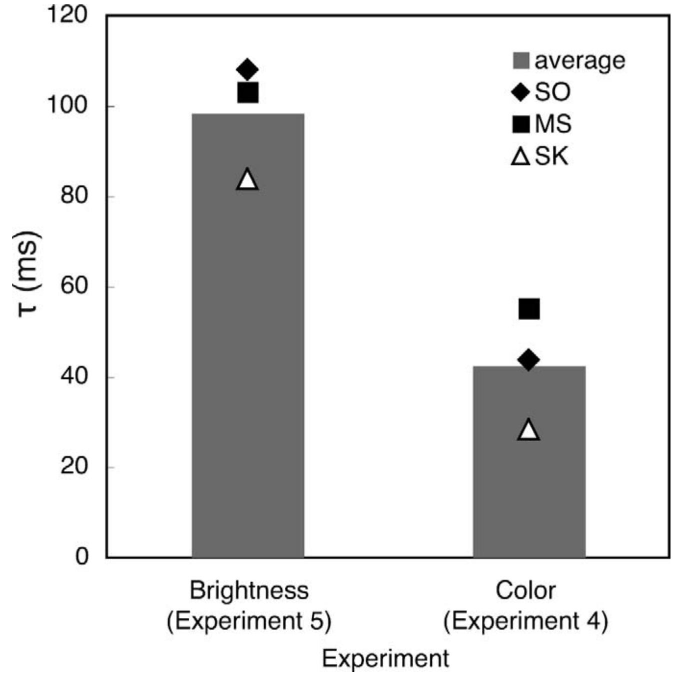

Figure 9. The τs (time constants) in Experiments 5 (brightness) and 4 (color). Different symbols represent different subjects.

General discussion

We investigated the spatial properties and dynamics of simultaneous contrast in brightness and color perception. Through the present series of experiments, we revealed similarities and dissimilarities between the two illusions.

Experiments 1 and 2 showed that both brightness contrast and color contrast were enhanced when the stimuli were presented very briefly. This suggests the existence of a mechanism that operates to estimate brightness and color only when the stimulus is brief. As for the spatial properties of the illusions, Experiments 1 and 3 demonstrated that in both cases, simultaneous contrast in a flashed stimulus was primarily based on local information across the center and surround because the enhancement of the illusion strength was abolished by inserting a spatial gap. As for the temporal properties, Experiments 4 and 5 showed that the mechanisms responsible for the strong illusion at short durations were narrowly tuned to brief durations. On the other hand, Experiment 3 revealed that the color contrast seen with long-lasting stimuli, unlike brightness contrast, was also greatly reduced by inserting a spatial gap. This implied that it also depended on local information, as did color contrast in flashed stimuli. Moreover, brightness contrast and color contrast had different temporal tuning functions; brightness contrast showed a consistently slower time course.

Models to reconcile the duration dependences of simultaneous brightness and color contrast

Robinson and de Sa (2008) reported that the magnitude of simultaneous brightness contrast decreased with increasing stimulus duration and argued that brightness perception may evolve over time. This relationship between the illusion and the stimulus duration was convincingly observed here. The present study further suggests that the processes involved in brightness perception at short durations differ from those involved at long durations. At short durations, the spatial gap reduced the illusion magnitude for both brightness and color. This implies that the local contrast information that exists along the border between the test and surround stimuli primarily contributes to the strong simultaneous contrast seen at short durations. However, at long durations, the gap width had no effect on the strength of brightness contrast. With a gap up to 1° in width, the illusion did not decrease but maintained the same strength as with no gap. This suggests that at long durations, luminance signals coming from a distance >1° affect the test area,

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and whether the surround shares the border with the test stimulus or not matters little. Based on the finding that the illusion had very different spatial properties under the 10-ms and 500-ms conditions, we argue that different processes are involved in brightness contrast depending on duration and that these processes have properties that differ both temporally and spatially.

On the other hand, such differences were not observed for color contrast. That is, the magnitude of the illusion became smaller as the gap became wider under both the 10-ms condition and the 500-ms condition, suggesting that local chromatic contrast information played a key role in both conditions. Therefore, there is no need to introduce another mechanism in addition to a quantitative difference caused by the dynamics of a single mechanism.

Considering the similarities and dissimilarities observed, we built simple models to express the difference between simultaneous brightness contrast and simultaneous color contrast:

$$f_{brightness}(t) = K_{b1}\exp(-t/\tau_1) + K_{b2}\{1-\exp(-t/\tau_2)\}, \tag{2}$$

$$f_{color}(t) = K_{c1}\exp(-t/\tau_1) + C. \tag{3}$$

Brightness perception (Equation 2) is expressed as a linear summation of two exponential curves of opposite polarities: The first represents a fast-responding process that is responsible for the enhanced illusion seen with flashed stimuli, and the second represents a slower component that produces the milder illusion seen with longer-lasting stimuli. Color perception (Equation 3), which did not show different spatial properties at different durations (Experiment 3), is expressed as a single exponential curve, which has the same form as Equation 1. The first component in Equation 2 and the exponential curve in Equation 3 share the common time constant τ_1. This constraint is arbitrarily introduced for simplicity. In the same vein, a constant C in Equation 3 is simply replaced by another exponential function in Equation 2, as if the asymptotic value of the illusion strength at sufficiently long durations were only ascribed to the asymptote of the second exponential. These arbitrary constraints are useful in determining model parameters for the particular data-fitting analysis shown below, but if they were relaxed, qualitatively similar arguments would still be viable. The key point is that adding the second component in the brightness case makes the resultant curve shallower. Thus, the greater τs, consistently found in the brightness experiment (Experiment 5), are explained by this simple summation model. Actual data from three subjects were well fitted by this model (Figure 10).

In the fitting process, we assumed the existence of two components; theoretically, however, the number of components could exceed two. Additionally, a variety of processes could be continuous rather than discrete. The ODOG model (Blakeslee & McCourt, 1999), which predicts not only simultaneous contrast but also other variations of brightness illusions, consists of different filters of various spatial scales. The original model did not mention different temporal characteristics of the filters. However, if we assume that the larger filters are more sluggish and the smaller filters are faster, the different components in our aforementioned model would be explained satisfactorily by the different filters in the ODOG model.

How does simultaneous contrast incorporate both fast and slow processes?

De Valois et al. (1986) (but see the Introduction) and Rossi and Paradiso (1996) both reported that when they used a temporally modulated inducer surrounding a test area, illusory modulation of the test stimulus was seen only when the inducer modulation rate was below ~3 Hz. This cut-off frequency was found for both the brightness- and color-contrast conditions. This finding was considered evidence that simultaneous contrast is a slow process.

If the simultaneous contrast is really "slow" as these studies suggested, how could we see the strong simultaneous contrast effect in our flashed stimuli? How can we reconcile the apparent difference between these studies and our own? At some point between stimulus input and our final perception, there is a bottleneck that slows the perception of simultaneous contrast. Where exactly does the bottleneck related to this perceptual slowing emerge in visual processing? One possibility is that a stimulus with a high temporal frequency is "invisible" to a spatially local interaction mechanism and is thus incapable of affecting the brightness/color of a surrounded region in the first place. However, this possibility does not seem very plausible because previous studies, such as those by Blakeslee and McCourt (2008) and D'Antona and Shevell (2009), offer evidence against it. D'Antona and Shevell (2009) used a dynamic inducer whose color was modulated in a compound waveform $f1+f2$, where $f1$ and $f2$ were high frequencies well beyond the cut-off frequency reported by De Valois et al. (1986). Induced color modulation was perceived at the frequency of $|f1 - f2|$ in a static test stimulus surrounded by the inducer. This result indicates that even if the modulation of the inducer is characterized by high frequency, the modulation pattern can induce simultaneous contrast. Together with these previous studies, the present study provides evidence against the above hypothesis. Thus, the bottleneck that prevents fast changes from appearing in the perception of simulta-

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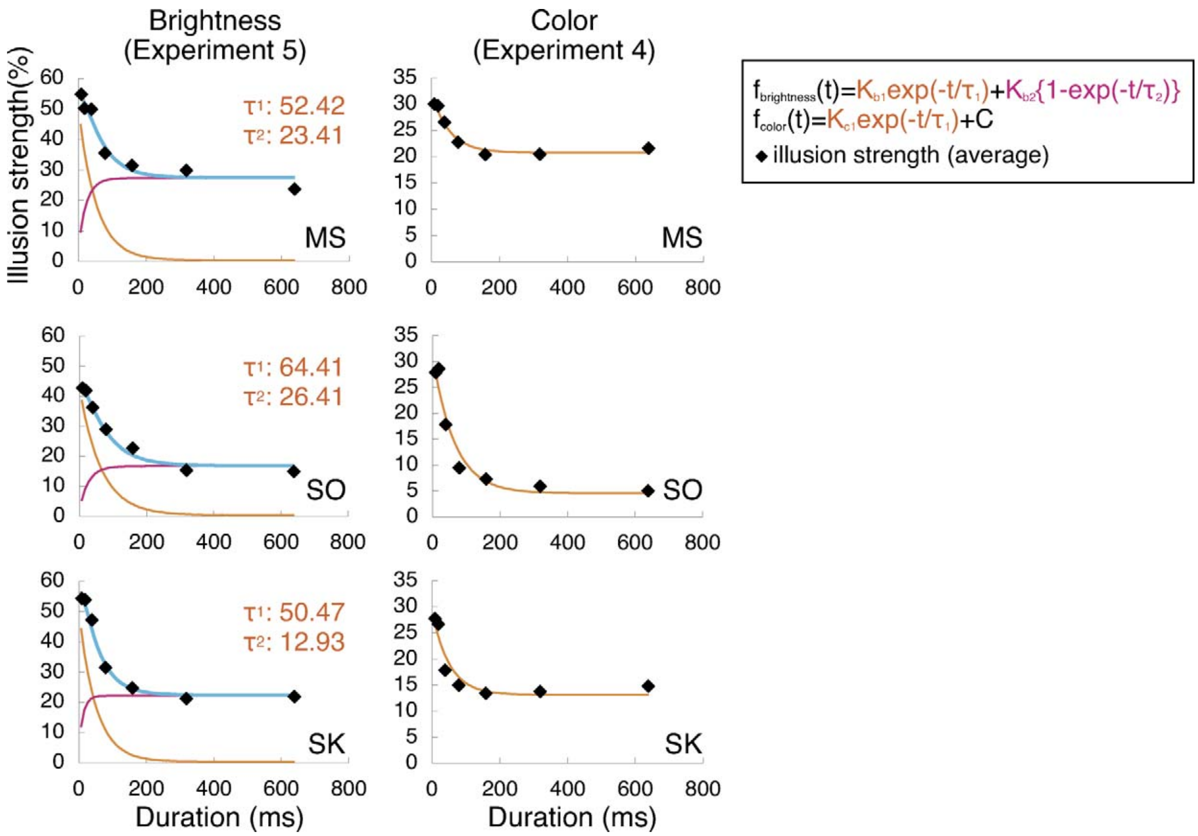

Figure 10. Average illusion strength for each of the three subjects who participated in both Experiments 4 and 5. Illusion strength is expressed as percent change in the appearance of the test stimulus and is averaged across the four surround conditions. The left and right columns represent brightness and color data, respectively. Time constants (ms) are shown in the left panels. The blue curve in the brightness data indicates the best-fit model using Equation 2. The orange curve in the color data indicates the best-fit model using Equation 3, i.e., a single decay function that shares the common shape with the first term of Equation 2. The orange and pink curves in the brightness data indicate the first and second terms, respectively, of Equation 2.

neous contrast is not located at the very first stage of spatial interaction.

We therefore assume that there should be a sluggish process after the initial spatial interaction that causes the final perception to be slower than the first crude calculation. We argue that, at some later stage, this sluggish process acts as the low-pass filter and that, after this process, information about the fast-alternating inducing stimulus disappears. This means that even in the display with rapid alternation, quickly alternating signals for simultaneous contrast emerge at the first spatial interaction only to dissolve at a later stage. This sluggish property may have been reflected in the results of De Valois et al.'s (1986) and Rossi and Paradiso's (1996) studies.

Previous studies have proposed several different candidates as the neural basis of simultaneous contrast. Rossi, Rittenhouse, and Paradiso (1996), for example, found cells responding to brightness rather than physical luminance or contrast in the primary visual cortex of cats. The responses of some cells were attenuated when the surround modulation rate was above 3 Hz, consistent with the cut-off frequency for brightness contrast. Human fMRI studies have also demonstrated activities correlated with perceived brightness or perceived color in the primary visual cortex (e.g., Pereverzeva & Murray, 2008; Sasaki & Watanabe, 2004). Additionally, one visual evoked potential study demonstrated that an early (less than 100 ms) component of visual processing was correlated with perceived brightness (McCourt & Foxe, 2004). On the other hand, neural responses to achromatic/chromatic physical flickers are known to have sensitivity to very high flicker rates that are perceptually irresolvable (Gur & Snodderly, 1997; Jiang, Zhou, & He, 2007; Lee, Martin, & Valberg, 1989). We argue that the first spatially local interaction can be activated by fast neural responses to brief stimulation. Under the 10-ms condition in our experiments, the stimulus duration itself was brief, but the rate of this flash was less than 2 Hz (roughly once in 500 ms). This is presumably below the cut-off frequency that De Valois et al. (1986) and Rossi and Paradiso (1996) reported. Thus, the spatial interaction process is fast enough to

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yield signals pertinent to simultaneous contrast, but these are subsequently averaged out during the sluggish process involved in the perception of brightness and color.

Fast spatial-interaction signals may serve an important role in detecting an object in noisy and dynamic scenes by instantaneously enhancing edges. However, when it comes to determining the brightness/color of the object, the contrast signal is not a perfect cue. The signals might inform us of a fast-changing contrast at the edge, but it is unlikely that an object's surface would change so rapidly in a realistic environment. Thus, attributing the rapidly changing contrast signal to a change in the surround, not in the object, would lead to a more reasonable estimation. The subsequent low-pass temporal filter process probably serves to prevent those signals from directly affecting the perceived brightness/color of the object (cf. D'Antona & Shevell, 2009).

In short, the apparent difference between the previous and the current studies can be explained in terms of the location of the bottleneck. If we assume a fast-responding local interaction mechanism and a slow-responding process, or a low-pass filter, that prevents the fast signal from the initial interaction from emerging into the final percept, the discrepancy between the two studies can be reconciled, as described above.

The Broca–Sulzer effect does not explain the strong illusion under the 10-ms condition

The perceived brightness of a flash depends on flash duration (Broca–Sulzer effect, also known as temporal brightness enhancement) and peaks at 50–150 ms. This duration dependence of brightness has been found not only in luminance increments but also in decrements (Björklund & Magnussen, 1979; White, Irvin, & Williams, 1980). A possible relationship between the Broca–Sulzer effect and the simultaneous contrast effect has been argued. Alpern (1963) found that the relationship between simultaneous brightness contrast and stimulus duration varied according to inducing luminance. For low-inducing luminance, the illusion strength increased with duration. However, as the inducing luminance became greater, the illusion strength peaked at shorter durations. This change was claimed to resemble the profile of the Broca–Sulzer effect. We argue, however, that it is neither likely nor sufficient that any Broca–Sulzer effect that might occur in the surround stimulus contributes to our findings. The illusion in our experiment was strongest at the surround duration of one display frame, rapidly decaying with increasing duration, whereas previous Broca–Sulzer studies have revealed that the peak of the illusion occurs at 50–150 ms (Björklund & Magnussen, 1979; Kittlerle & Corwin, 1979; White et al., 1980). Also, previous studies have shown virtually no evidence of a chromatic version of the Broca–Sulzer effect (Bowen & Nissen, 1979; Osaka, 1986). Therefore, the Broca–Sulzer effect does not provide a viable account for the enhanced simultaneous contrast observed in the present study.

Other illusions

As we mentioned in the Introduction section, some illusions appear to have special mechanisms for stimuli of brief duration. The COC illusion is one case in which brightness is highly dependent on edge luminance information; in this sense, this illusion is similar to simultaneous contrast. Indeed, duration dependency similar to that in the present study has been observed in the COC illusion as well; the illusion strength peaked at a short (33 ms) duration, dropped at moderate (125 ms) duration, and remained at a low level with long (500 ms) duration for both achromatic and chromatic versions of the COC illusion (Wachtler & Wehrhahn, 1997). Furthermore, an experiment similar to that by De Valois et al. (1986) was conducted for the COC illusion, and a similar cut-off frequency at a few hertz was found (Devinck, Hansen, & Gegenfurtner, 2007). These findings may suggest that the same principle is involved in the COC illusion and simultaneous contrast.

The present study investigated the spatiotemporal properties of simultaneous contrast effect of brightness and color, but other simultaneous contrast effects also exist in various domains, such as spatial frequency (Klein, Stromeyer, & Ganz, 1974), orientation (tilt), luminance contrast (Chubb, Sperling, & Solomon, 1989), and size (Ebbinghaus illusion). Among them, the tilt illusion exhibits a similar temporal profile to our findings. Wenderoth and Johnstone (1988), using grating stimuli, showed that the tilt illusion decreased as test duration increased up to approximately 100 ms and then leveled off (see also Wenderoth & van der Zwan, 1989). Westheimer (1990) also showed a similar temporal profile of the tilt illusion using line stimuli. It is therefore possible that the computational principle responsible for the effects found in the present study is also involved in other simultaneous contrast effects.

Higher-order factors of brightness and color

In this study, we used simple center–surround stimuli to investigate the spatiotemporal properties of simultaneous brightness/color contrast, focusing particularly on the fast interaction between two adjacent areas that

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is reasonably conceived to happen at an early stage of brightness and color processing. In contrast, it is widely known that in addition to edge contrast, other factors that involve more complex, higher-level analyses of images that could not be explained by simple local interactions can also affect brightness/color perception in a global context. These analyses include the articulation and variance in brightness/color in surrounding areas (Brown & MacLeod, 1997; Lotto & Purves, 1999; Schirillo & Shevell, 1996), interpretation of three-dimensional configuration (Adelson, 1993; Gilchrist, 1977; Lotto & Purves, 1999), and color memory of familiar objects (Hansen, Olkkonen, Walter, & Gegenfurtner, 2006), to name a few. Because our research aims to assess low-level interactions and is not focused on the contribution of these other factors, we simply mention that these could affect our perception in more complicated, realistic visual environments. Furthermore, parts of the mechanisms deemed low-level in our terms might also play a role in these apparently intelligent computations. At least it is safe to say that our 10-ms condition is a special case in which the visual system is forced to estimate the appearance of the test region without using all the cues mentioned above. Also, a longer time period than that necessary for edge detection by an early-stage process may be required to use those cues. Therefore, if the stimulus is briefly flashed, as in our experiments, the only cue available to the system is the luminance/color difference along the edge. This cue-poor situation is why we observed the enhancement of illusion strength under the 10-ms condition. As other cues become more available with increasing duration, brightness/color perception is revised to become more compatible with those other cues. This process of revision is probably reflected in the exponential decay seen in our data (Experiment 5) and is probably one of the possible sluggish processes that may slow down the final percept.

Conclusions

Simultaneous brightness contrast and simultaneous color contrast are not only perceived but also enhanced in the case of a flashed stimulus. Thus, textbook demonstrations of simultaneous contrast only include perceptions that have been finalized through complex scene interpretation. Therefore, the induction of brightness and color from surround to center is fast in the sense that it does not require that sensory evidence from the surround accumulate over time. The apparent sluggishness of simultaneous contrast demonstrated previously emerges after the initiation of spatially local interactions between adjacent areas that must constitute the first step in the process of simultaneous contrast.

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