Bidirectional aftereffects in perceived contrast

Wakana Hata
Department of Integrated Sciences, The University of Tokyo, Tokyo, Japan

Isamu Motoyoshi
Department of Life Science, The University of Tokyo, Tokyo, Japan

It is well known that prolonged observation of a high-contrast stimulus alters the perception of a subsequent test stimulus. Previous studies of perceived contrast shifts only reported perceived contrast reductions. Here, we used successive presentations of test and reference stimuli and found that perceived contrast was reduced if tests had a lower contrast than adaptors but was significantly enhanced when tests had a higher contrast than adaptors. Such bidirectional contrast aftereffects were not observed for single adaptor flashes but became increasingly pronounced for repeated adaptor presentations, thereby suggesting that the aftereffect is a consequence of adaptation rather than of attentional cuing or temporal repulsion. In addition, perceived contrast reduction weakened as we increasingly jittered the spatial position of the adaptor, but perceived contrast enhancement was observed for large spatial range of jittered adaptor positions. We conclude that aftereffects involve adaptation in distinct mechanisms with narrow and broad spatial tunings. Results suggest that the visual system not only possesses low-level contrast encoding units, which monotonically increase their responses as physical contrast increases, but is also equipped with high-level channels selectively tuned for particular contrast ranges.

Introduction

Prolonged observation of a particular visual stimulus alters the perception of a subsequent stimulus. This effect of adaptation, called aftereffect, has been reported for a variety of visual attributes such as orientation (Gibson & Rander, 1937), spatial frequency (Blakemore, Nachmias, & Sutton, 1970), color (Webster & Mollon, 1991), direction of a motion (Levinson & Sekuler, 1976), face (Webster, Kaping, Mizokami, & Duhamel, 2004; Webster & Maclin, 1999), aspect ratio (Regan & Hamstra, 1992), texture density (Durgin, 1995; Durgin & Huk, 1997; Durgin & Proffit, 1996), and duration (Heron et al., 2012). Common to these perceptual phenomena is that the aftereffect is shifted in the direction opposite to the adaptor along the adapting dimension. Such bidirectional and repulsive perceptual shifts are the hallmark signature of population coding models—theoretical frameworks in which perceptual aftereffects are determined by the distribution of neural responses over channels selectively tuned to values along a particular stimulus dimension such as orientation (Blakemore, Carpenter, & Georgeson, 1970).

Aftereffects are known to occur for luminance contrast as well, but unlike the aforementioned cases, contrast aftereffects reported in the literature have been strictly unidirectional. In fact, although prolonged observation of a high-contrast adaptor reduces the perceived contrast of subsequent test (Blakemore, Muncey, & Ridley, 1973; Georgeson, 1985; Ross & Speed, 1996; Sato, Motoyoshi, & Sato, 2016), perceived contrast is not enhanced if test contrast is higher than the adaptor's. For example, Hammett, Snowden, & Smith (1994) systematically examined perceived contrast for various test contrasts after adaptation and found that perceived contrast was reduced for low-contrast tests but remained largely veridical for higher-contrast tests. Contrast adaptation, or the contrast aftereffect, is typically thought to reflect a reduction in the gain of early visual units whose response increases monotonically with image contrast (Määttänen & Koenderink, 1991; Ohzawa, Sclar, & Freeman, 1982).

In the present study, we report *bidirectional* contrast aftereffects in experiments where repeated presentations of an adaptor are interspersed with blanks and where test and reference stimuli are presented sequentially (Experiments 1 and 2). Aftereffects became increasingly pronounced with repeated adaptor presentations, and no effect was observed if the adaptor was flashed only once. These findings suggest that the aftereffect is a consequence of prolonged exposure to the adaptor rather than a product of attentional cuing or momentary temporal repulsion. We further examined bidirectional aftereffects for adaptors presented

Citation: Hata, W., & Motoyoshi, I. (2018). Bidirectional aftereffects in perceived contrast. *Journal of Vision*, *18*(9):12, 1–13, https://doi.org/10.1167/18.9.12.

https://doi.org/10.1167/18.9.12 Received March 23, 2018; published September 11, 2018 ISSN 1534-7362

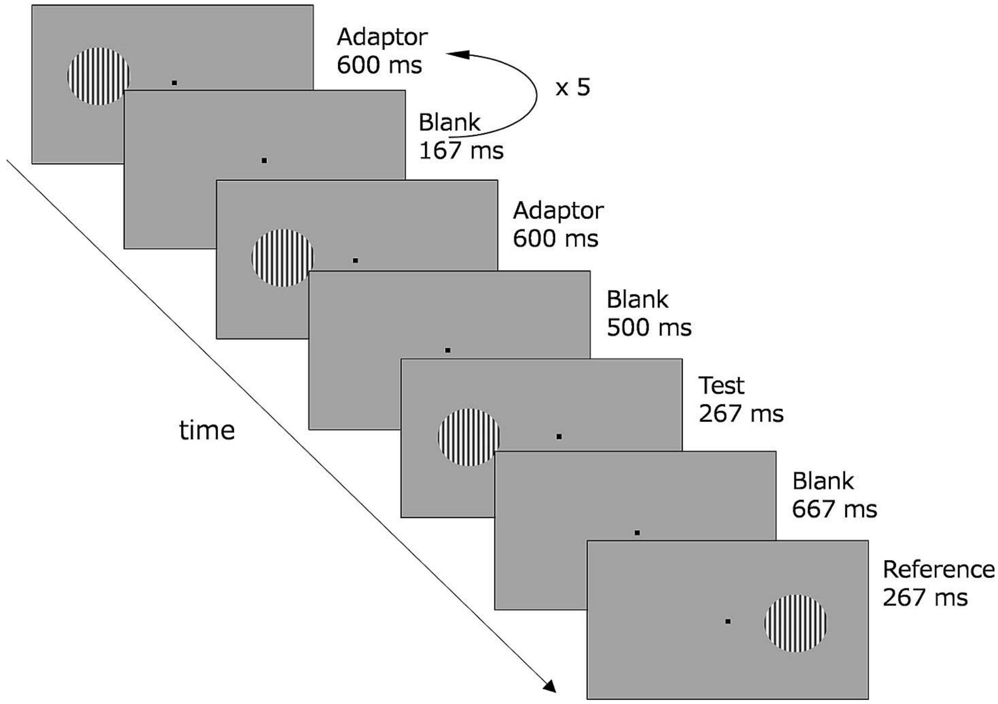

Figure 1. Experiment stimulus sequence. An adaptor stimulus was flashed repeatedly either in the right or left field of the display. After a blank, a test stimulus was presented at the adapting location. Following a blank of 667 ms, a reference stimulus was then presented in the opposite field.

over a range of spatial extents and found that perceived contrast reduction remained relatively local but that perceived contrast enhancement was relatively global. These results lead us to suggest that adaptation to a particular contrast results in *two* aftereffects: the first is a reduction in perceived contrast attributable to gain control in low-level contrast encoding units (i.e., classic contrast adaptation), and the second is a bidirectional shift in perceived contrast due to sensitivity reduction in higher-level neural channels selectively tuned to a particular contrast level.

Experiment 1

Methods

Observers

One of the authors (WH) and five naïve observers participated in the experiment, and all had normal or corrected-to-normal vision. All experiments followed the guideline outlined by the ethics committee for experiments on humans at Graduate School of Arts and Science (University of Tokyo), and observers provided informed written consent in accordance with the Declaration of Helsinki.

Apparatus

Visual stimuli were generated by a computer (Dell Precision T1600; Dell Inc., Round Rock, TX) and displayed on a 27-in. LCD monitor (BenQ XL2730Z; BenQ Co., Taipei, Taiwan) with a refresh rate of 60 Hz. From a viewing distance of 60 cm, the LCD's pixel resolution was 1.8 min/pixel. The luminance of the LCD monitor was carefully calibrated by means of a colorimeter (CRS ColorCal II; Cambridge Research Systems, Ltd., Kent, UK) and controlled along a virtually continuous scale by the Noisy-Bit technique (Allard & Faubert, 2008).

Stimuli

The visual display was composed of an adaptor, a test stimulus, and a reference stimulus. All stimuli consisted of vertically oriented sinusoidal grating patterns drawn within a circular sharp-edged 6 degree-diameter window (Figure 1). Gratings had a spatial frequency of 2.1 c/° and assumed a random spatial phase. Grating mean luminance matched the mean luminance of the homogenous gray background of 57.3° × 32.2°.

Procedure

The perceived contrast of the test stimulus was measured by a two-alternative forced-choice procedure.

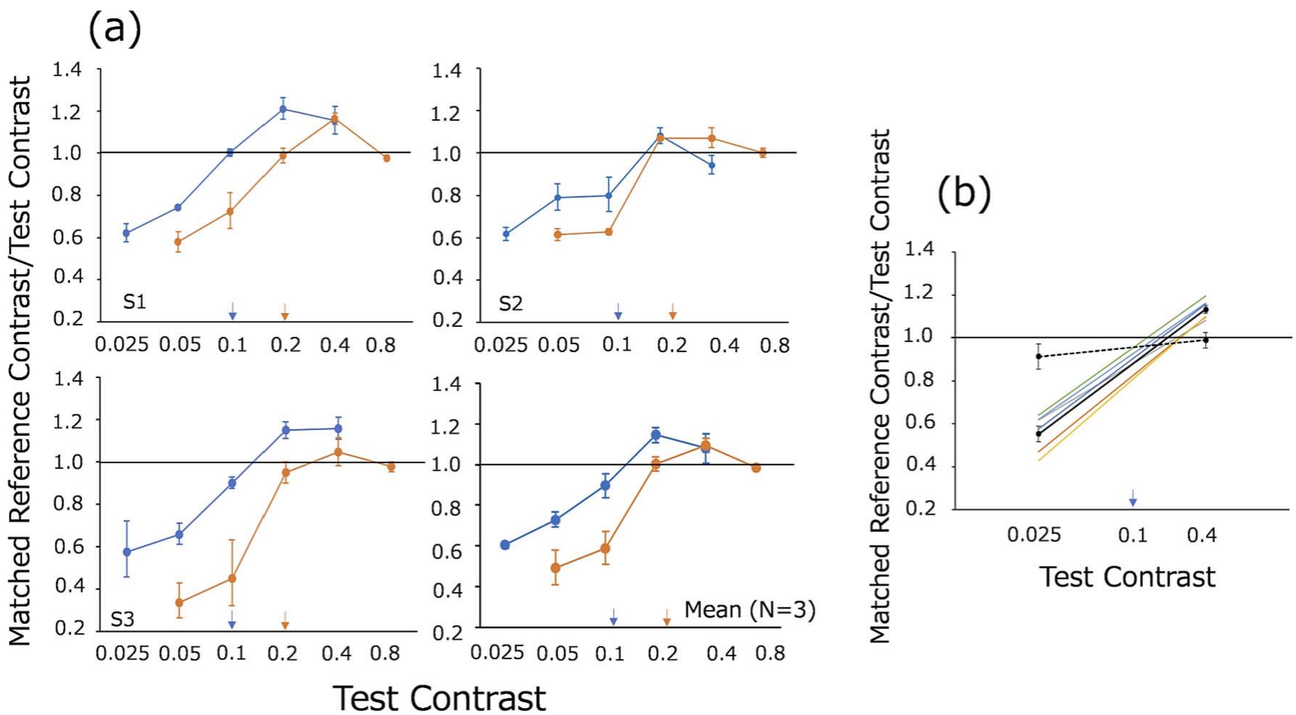

Figure 2. Bidirectional contrast aftereffects. The horizontal axis represents physical test contrast. The vertical axis represents perceived test contrast (postadaptation). (a) Perceived contrast values are plotted relative to physical contrast where a value of 1 stands for the physical contrast of test stimulus. Blue and red symbols correspond to adaptor contrasts of 0.1 and 0.2, respectively. Arrows indicate the contrast of the adaptor for each plot. Error bars represent ±1 *SE*. The right panel (b) shows the results for two test contrasts from six observers. Colored lines represent the results following adaptation to a contrast of 0.1 and the black line represents the average. Dashed black line represents the average of the same six observers in the no-adapt condition. Error bars represent ±1 *SE*.

A fixation point was presented in the center of the display. At the beginning of each trial, an adaptor was repeatedly presented at either left or right location separated by 5.4° from the fixation point. The adaptor was presented for 600 ms with an interstimulus interval of 167 ms. This duration was chosen as it seemed optimal to elicit postadaptation enhancement in the perceived contrast in our display.

On every presentation, the center of the adaptor was randomly jittered within a virtual square area of 2° × 2°. Following a blank of 500 ms after adaptor offset, the test stimulus was presented at 5.4° from the fixation point for 267 ms. Following another blank of 667 ms, the reference stimulus was presented on the other side of fixation for 267 ms.

On each trial, after the offset of all stimuli, observers were asked to press one of two buttons to indicate which of the two stimuli, either the test or the reference stimulus, appeared to have a higher contrast. The contrast of the reference stimulus was varied in accordance with a staircase procedure. The contrast of the reference stimulus was reduced by a factor of 0.9 after the observers judged that the reference stimulus had a higher contrast and was increased by a factor of 1.1 when the observer judged that the test stimulus had a higher contrast. On the first trial in each session, the contrast of the reference stimulus was the same as that of test stimulus. No feedback was given. The next trial started immediately after the response.

The adaptor was presented 10 times prior to each session and was interleaved by blanks. The contrast of the adaptor remained fixed within each measurement block. For three observers, the contrast of the adaptor was either 0.1 (test contrast varied between 0.025 and 0.4) or 0.2 (test contrast varied between 0.05 and 0.8). For the other three observers, the contrast of the adaptor was 0.1 (test contrast was either 0.025 or 0.4). In both cases, test contrasts were randomly interleaved. After the experiment, the point of subjective equality (PSE) for perceived test contrast was estimated by means of the maximum likelihood method based on at least 120 trials per observer. Standard error for individual data was calculated by a bootstrap of 4,000 samples.

Results

Figure 2a plots perceived test contrast as a function of physical test contrast for three of six observers. Perceived contrast is expressed relative to the physical contrast of the test stimulus such that values smaller than 1 indicate that perceived post-adaptation contrast is reduced whereas values larger than 1 indicate that perceived postadaptation contrast is enhanced. Blue and red symbols represent results adaptations to 0.1 and 0.2 contrasts, respectively. The right bottom panel in Figure 2a shows the arithmetic mean across observers in which error bars represent standard error. The contrast of each adaptor is indicated by an arrow. Results show that perceived contrast is reduced if test contrast is lower than adapting contrast but that perceived contrast is enhanced if test contrast is higher than adapting contrast.

For adaptors of 0.1 contrast, perceived contrast was reduced for test contrast of 0.025 but enhanced for test contrasts of 0.4 (Figure 2b). We also conducted a control experiment in which the six observers matched test contrasts of 0.4 and 0.025, respectively, without adaptation. We found clearly significant differences between the adapt and no-adapt conditions (two-tailed paired *t* test; $t(5) = 5.1$, $p < 0.005$ for 0.025 test contrast; $t(5) = 4.0$, $p < 0.01$ for 0.4 test contrast).

Data from Experiment 1 reveal bidirectional contrast aftereffects, although perceived contrast reduction is relatively larger than perceived contrast enhancement. Inspection of curves in Figure 2a suggests that perceived contrast results from the combined influence of two separate aftereffects: 1—a classical post-adaptation contrast reduction, and 2—a bidirectional contrast repulsion. Under this dual-aftereffect hypothesis, the repulsive component would reduce perceived contrast if test contrast is lower than adapting contrast but increase perceived contrast if test contrast is higher. The classical postadaptation component would be unidirectional and reduce perceived contrast only if test contrast is lower than adapting contrast (Georgeson, 1985; Hammett et al., 1994). Together, these two hypothetical components could explain the bidirectional asymmetry shown in Figure 2a. By direct analogy with theories on other aftereffects such as tilt aftereffect and size aftereffect (Blakemore & Sutton, 1969; Gilbert & Wiesel, 1990), the bidirectional component hinted at by our data may point to a higher-level neural representation of contrast operating along the lines of repulsive population codes. Such a higher-level representation would be distinct from lower-level representations in which adaptation results only in contrast gain reductions (Movshon & Lennie, 1979; Sclar, Lennie, & DePriest, 1989; Wilson & Humanski, 1993).

Experiment 2

Contrast enhancement, whereby the contrast of a test is perceived as higher than the physical contrast of an adaptor, has not been reported in previous studies, and so it is natural to ask why perceived contrast enhancement was observed in ours. A significant procedural difference between previous studies and the current one concerns the temporal sequence of test and reference stimuli presentations. Recent studies have shown that aftereffects for dot texture density is unidirectional for simultaneous tests and references but bidirectional for successive tests and references (Sun & Baker, 2017). On the basis of these findings, it is conceivable that contrast enhancement manifested itself only in our study because tests and references were presented at different moments in time.

To examine this possibility, we measured perceived contrast for two types of stimulus presentations, namely simultaneous and successive test reference stimuli. If relative timing between test and reference plays an important role in contrast enhancement, then we would expect little or no enhancement in perceived contrast when test and reference stimuli are presented simultaneously.

Methods

The perceived contrast of test stimuli was measured by a two-alternative forced choice. Importantly, test and reference stimuli were presented simultaneously following the adaptor. As in Experiment 1, test stimuli were presented in the same position as the adapting stimuli, and reference stimuli were presented on the other side of fixation. The contrast of the adapting stimuli was 0.1 and the contrast of test stimuli was 0.025 or 0.4. Observers were one of the authors (WH) and three of the naïve ones who also participated in Experiment 1. The other experimental conditions were the same as in Experiment 1.

Results

Figure 3 plots perceived test contrast (y-axis) as a function of relative timing (i.e., simultaneous vs. successive) between test and reference presentations (x-axis). Perceived contrast (postadaptation) is expressed as a ratio of physical test contrast so that a perceived-contrast value of 1 implies a veridical match. Results are shown for tests whose contrast was lower (blue) or higher (red) than the adaptor. We also conducted a control experiment in which the four observers matched test contrasts of 0.4 and 0.025 without adaptation for successive and simultaneous test/reference presentation, respectively.

Under conditions where test contrast was lower than the adaptor (blue), we found the expected reduction of perceived contrast compared with the control (no-adapt) condition regardless of whether test and reference stimuli were presented successively (as in Experiment 1)

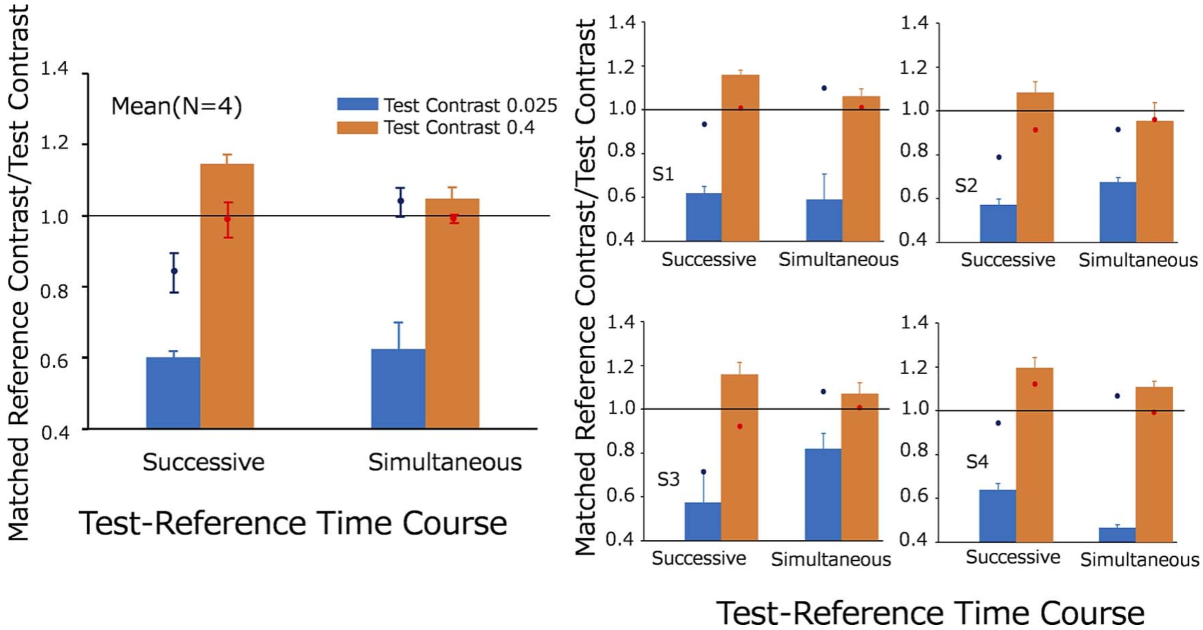

Figure 3. Perceived contrast as a function of relative timing between test and reference presentations. Perceived test contrast (y-axis) is plotted as a function of relative timing (i.e., simultaneous vs. successive) between test and reference presentations (x-axis). Perceived contrast (postadaptation) is expressed as a ratio of physical test contrast so that a perceived-contrast value of 1 implies a veridical match. Results are shown for tests whose contrast was lower (blue) or higher (red) than the adaptor. Blue and red circles in each panel represent the results in the control condition for test contrasts of 0.025 and 0.4, respectively. Error bars represent ±1 *SE*.

or simultaneously (two-tailed paired *t* test; $t(3) = 4.5$, $p < 0.05$ for simultaneous presentations, $t(3) = 3.3$, $p < 0.05$ for successive presentations). On the other hand, when test contrast was higher than the adaptor (red), we found significant perceived contrast enhancement compared with the control condition for successive test/reference presentations ($t(3) = 4.7$, $p < 0.05$) but no evidence of enhancement for simultaneous presentations ($t(3) = 2.3$, $p = 0.1$). The effects of enhancement in simultaneous and successive conditions were also significantly different from each other (two-tailed paired *t* test; $t(3) = 9.7$, $p < 0.005$). Qualitatively, the same results were obtained when the statistical tests were done for logarithmic values. The purpose of this experiment was to examine whether timing of the presentation altered the effect of enhancement. Thus, we only performed an analysis on enhancement. In short, perceived contrast enhancement effects are only observed for successive test and reference presentations.

These result suggests that the relative timing of stimulus presentations is one of the primary factors determining perceived postadaptation contrast enhancement.

Experiment 3

A key question is whether perceived contrast enhancement is genuinely caused by adaptation. Previous studies have shown that the perception of shape and orientation shifts in a direction opposite to that given by a stimulus flashed immediately before (Suzuki & Cavanagh, 1998). It has been suggested that such perceptual shifts reflect the workings of high-level shape processing mechanisms concerned with aspect ratios and complex global shape patterns. In addition, the perception of dot motion (Anstis & Ramachandran, 1987; Ramachandran & Anstis, 1983) and facial expressions (Yoshikawa & Sato, 2008) is biased away from veridical in a way that emphasizes the difference between the current target and the preceding stimulus—a form of visual inertia. One hypothesis, then, is that perceived contrast enhancement operates along principles similar to those driving illusory temporal repulsions—that is, the last adaptor induces an enhancement in the perceived contrast of a subsequent higher-contrast test.

An alternative hypothesis is that attention could drive contrast enhancement. The perceived contrast of a grating is enhanced by if attention is directed to it by a spatial cue (Carrasco, Ling, & Read, 2004; Carrasco, Penpeci-Talgar, & Eckstein, 2000). It is therefore possible that the adaptor plays the role of a spatial cue and enhances the perceived contrast of the subsequent test stimulus. Perceived contrast reduction (which occurs when test contrast is lower than the adaptor's) would still manifest itself if the effects of low-level adaptation were strong enough to overwhelm the contrast-enhancing effects of attention.

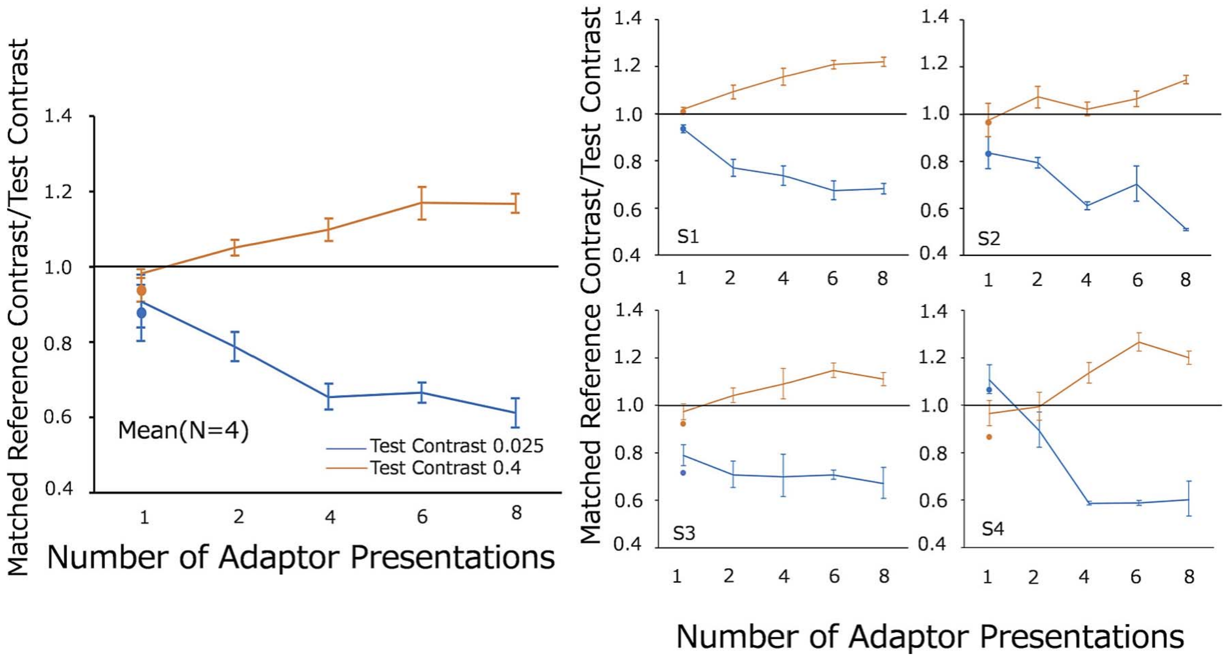

Figure 4. Perceived contrast aftereffect as a function of number of adaptor presentations. The horizontal axis shows the number of adaptor presentations and the vertical axis represents relative perceived test contrast after adaptation. Blue and red curves show results for test contrasts of 0.025 of 0.4, respectively. Blue and red markers on the left side of each panel represent results of no-adapt condition for test contrasts of 0.025 and 0.4, respectively. Error bars represent ±1 *SE*.

To test these possibilities further, we varied the number of presentations for the adaptor. If contrast enhancement results from short-term temporal contrast repulsion or attentional cuing, a single presentation of the adaptor should suffice to elicit an enhancement in perceived contrast. If, however, contrast enhancement is the manifestation of an adaptive process, one would expect that only repeated and prolonged exposure to an adaptor would succeed in driving the effect.

Methods

Perceived test contrast was measured after a variable number of adaptor presentations. The contrast of the adaptor was 0.1 and the contrast of the test stimulus was 0.025 or 0.4. There was no initial adaptation at the beginning of the session. The number of presentations of the adaptor at the beginning of each trial was varied from 1 to 8. The number of presentations of the adaptor was fixed within each measurement block. Observers were one of the authors (WH) and three naïve students. The PSE was determined based on at least 120 trials, except for two based on at least 85 trials. The first five trials in each block were excluded from the analysis. The other experimental conditions were the same as in Experiment 1.

Results

Figure 4 plots perceived test contrast (y-axis) as a function of the number of adaptor repetitions (x-axis). As before, perceived test contrast is expressed as a ratio of the test's physical contrast so that a value of 1 corresponds to a veridical match. Results show there was no aftereffect when the adaptor was presented only once but the aftereffect became stronger as the number of adaptor presentations increased. A two-factor analysis of variance (ANOVA) on perceived contrast, with test contrast and adaptor repetition as factors, revealed a significant effect of test contrast ($F(1) = 13865.4$, $p < 0.001$). The interaction between test contrast and adaptor repetition was also significant, ($F(4) = 9.3$, $p < 0.01$). Simple main effects on the number of adaptor repetition were significant for both test contrasts ($F(4, 12) = 7.0$, $p < 0.01$, test contrast = 0.025; $F(4, 12) = 9.5$, $p < 0.01$, test contrast = 0.4). We also conducted a control experiment in which the four observers matched test contrasts of 0.4 and 0.025, respectively, without adaptation. For a test contrast of 0.4, we found clearly significant differences between the adapt and no-adapt conditions for all adaptor repetitions except for the single adaptor presentation (two-tailed paired t test; $t(3) = 10.9$, $p < 0.01$, for two repetitions; $t(3) = 3.6$, $p < 0.05$, for four repetitions; $t(3) = 3.7$, $p < 0.05$, for six repetitions; $t(3) = 6.3$, $p < 0.01$, for eight repetitions).

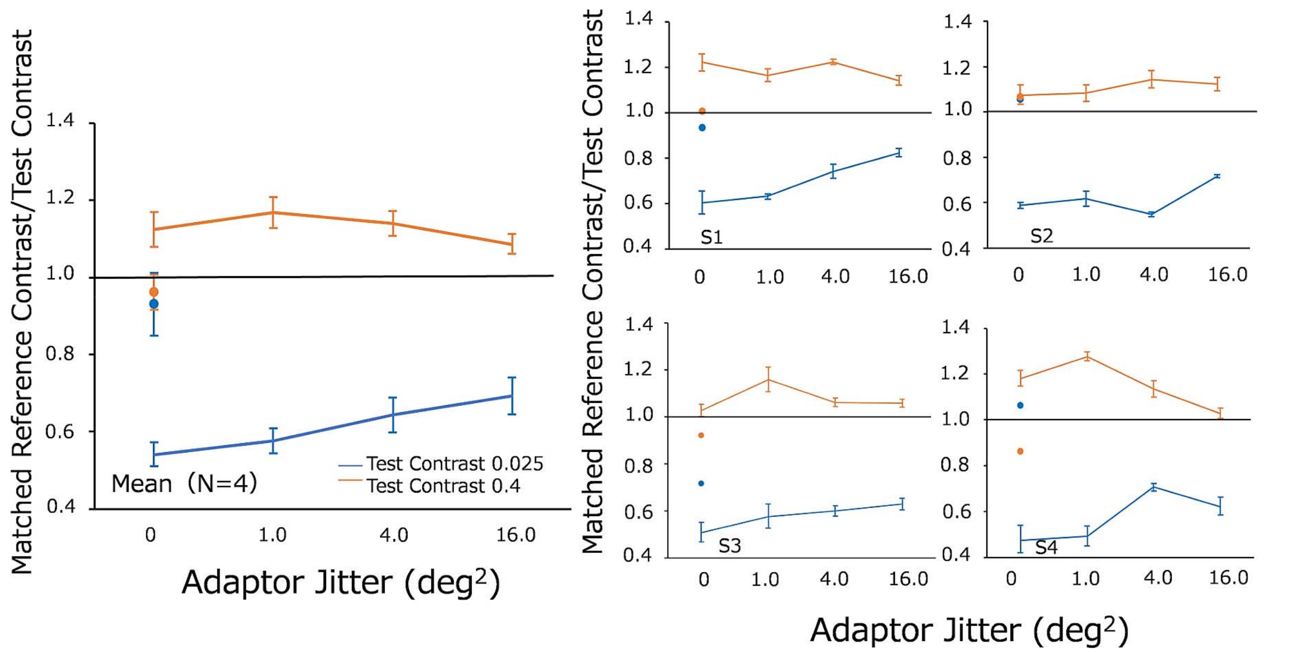

Figure 5. Perceived test contrast (y-axis) as a function of adaptation field size (x-axis). Perceived contrast is expressed as a ratio of physical test contrast so that a value of 1 implies a perfect match. Blue and red curves show results for test contrasts of 0.025 and 0.4, respectively. Blue and red circles on the left side in each panel represent the results of no-adapt condition for test contrasts of 0.025 and 0.4, respectively. Error bars represent ±1 *SE*.

The observed reduction in perceived contrast is consistent with the one found in many past studies where the effect of adaptation in early visual units increases as a function of a total adaptation duration (Greenlee, Georgeson, Magnussen, & Harris, 1991; Hammett et al., 1994). By comparison, it is difficult to explain that contrast enhancement becomes stronger with repeated adaptor presentations on the basis of temporal repulsion effects or attentional cueing as a single presentation of the adaptor would be sufficient to induce significant aftereffects. Our results suggest therefore suggest that contrast enhancement is attributable to adaptation.

Experiment 4

Results from the three experiments above suggest that bidirectional shifts in perceived contrast are a consequence of adaptation in neural channels that are higher up in the visual processing hierarchy than early contrast-sensitive units that only work to reduce perceived contrast. In addition, physiological studies have suggested that, while neurons in the early visual cortex have small receptive fields, neurons in higher cortex have comparatively larger receptive fields (Smith, Singh, Williams, & Greenlee, 2001; Zeki, 1978). A prediction, then, is that mechanisms mediating bidirectional contrast aftereffects are spatially broad. To test this prediction, we measured perceived test contrast and manipulated the size of the adaptation field (the virtual square area over which adaptors were jittered). If higher-level processes underlie bidirectional aftereffects, then the magnitude of the contrast aftereffect should remain relatively constant over a substantial range of adaptive field sizes.

Methods

We measured perceived test contrast for spatial adaptation fields of variable size. The contrast of the adaptor was 0.1 and the contrast of test stimulus was either 0.025 or 0.4. The size of the adaptation field, which remained fixed within each experimental block, was either 0, 1.0, 4.0, or 16.0 degrees^2. The adaptation field of 4.0 degrees^2 was identical with those in Experiment 1, 2, and 3. One of the authors (WH) and three naïve observers participated in the experiment. The other experimental conditions were the same as in Experiment 1.

Results

Figure 5 plots relative perceived test contrast (y-axis) vs. the size of the adaptation field (x-axis). When the contrast of the test stimulus was lower than the adaptor's (blue curves), we found that perceived contrast reduction weakens as the spatial size of the adaptation field increases. By comparison, when the contrast of the test stimulus was higher than the adaptor's (red curves), perceived contrast enhancement appears relatively constant over all adapting field sizes on average. In fact, between the smallest jitter and the largest jitter, the difference in enhancement was about 3% on an average, whereas contrast reduction was weakened by about 28%.

A two-factor ANOVA on perceived contrast, with test contrast and adaptation field size as factors, revealed a significant effect of test contrast ($F(1) = 520.7$, $p < 0.001$). The interaction between test contrast and adaptation field size was also significant, ($F(4) = 3.8$, $p = 0.05$). The simple main effect of test contrast was significant for all adaptation field sizes ($F(1) = 138.3$, $p < 0.005$, for 0°; $F(1) = 74.4$, $p < 0.005$, for 1.0°; $F(1) = 188.5$, $p < 0.001$, for 4.0°; and $F(1) = 253.8$, $p < 0.001$, for 16.0°). The effect of adaptation field size was significant for a test contrast of 0.025 ($F(3) = 5.17$, $p < 0.05$), but not for a test contrast of 0.4 ($F(3) = 1.21$, $p = 0.23$). We also conducted a control experiment in which the four observers matched test contrasts of 0.4 and 0.025, respectively, without adaptation. For a test contrast of 0.4, we found clearly significant differences between the adapt and no-adapt conditions for adaptation field size of 4.0° (as Experiment 1, 2, and 3) and 16.0° (two-tailed paired t test; $t(3) = 4.0$, $p < 0.05$, for 4.0°; $t(3)= 5.2$, $p < 0.01$, for 16.0°). However, for adaptation field size of 0° and 1.0°, the difference between the adapt and no-adapt conditions were not significant (two-tailed paired t test; $t(3) = 2.4$, $p = 0.1$, for 0°; $t(3) = 2.7$, $p = 0.09$, for 1.0°). Thus, the enhancement effect is lost or reduced when the spatial range of adaptation is very narrow. We will discuss this point in the Discussion section.

The aforementioned results support the hypothesis that high-level mechanisms, which have larger spatial receptive fields, are involved in bidirectional contrast aftereffects. It is known that adaptation in early visual units induces perceived contrast reduction over a relatively small spatial range (but the range is a little larger than for contrast threshold elevation; see Snowden & Hammett, 1996), we suggest that adaptation in high-level mechanisms with larger receptive fields induce bidirectional shifts in perceived contrast over a broader spatial range.

Discussion

The present study has produced three important findings. First, we have demonstrated that the perceived contrast of a test is either enhanced or reduced if preceded by an adaptor whose contrast is respectively lower or higher than the adaptor's (Experiment 1). We observed this bidirectional contrast aftereffect in conditions where test and reference stimuli were presented successively, but no such effect was manifest in conditions where test and reference stimuli were simultaneous as in previous studies (Experiment 2). Therefore, we suggest that postadaptation contrast enhancement cannot be explained by classical contrast adaptation mechanisms that, by definition, predict only reductions in perceived contrast (Movshon & Lennie, 1979; Ohzawa et al., 1982). Second, the contrast aftereffect was not manifest for single presentations of an adaptor but grew in magnitude with additional presentations of the adaptor (Experiment 3). It is thus difficult to ascribe the phenomenon entirely to the effects of either temporal contrast (Suzuki & Cavanagh, 1998) or attentional cueing (Carrasco et al., 2004) as such mechanisms would likely only require a single presentation of the adaptor to elicit an aftereffect. Third, perceived contrast enhancement was observed for a large spatial range of jittered adaptor positions, but contrast reduction was substantially weakened as the spatial size of the adaptation field increased (Experiment 4). Our results therefore suggest the possibility that contrast-enhancement, as revealed by bidirectional contrast aftereffects, is mediated by adaptation in neural processes that reside higher up in the visual hierarchy than classical lower-level adaptation mechanisms generally believed to underlie perceived contrast reduction.

Data obtained in the present study seem to indicate that bidirectional contrast aftereffects involve two components: 1—a perceived contrast reduction via adaptation in low-level mechanisms, and 2—perceived contrast shifts via adaptation in higher-level mechanisms. However, higher-level adaptation shifts are expected to elicit not only contrast enhancements but also contrast reductions—a bidirectional property characteristic of repulsive-type aftereffects. Reviewing results in Experiment 1 (see Figure 2a), one can see that perceived postadaptation contrast peaks for test contrasts that are somewhat higher than the adaptor's and decreases at higher test contrasts. This general pattern is also found in repulsive aftereffects along various stimulus dimensions such as orientation, spatial frequency, direction of motion, and hue (Blakemore, Nachmias, & Sutton, 1970; Webster & Mollon, 1991). In Experiment 4, while contrast reduction decreases with adapting field size (a finding we attribute to local lower-level contrast adaptation), we nonetheless observed contrast enhancement for large spatial range (4.0 and 16.0 degrees^2) of jittered adaptor positions (Figure 5). The perceived contrast enhancement was not significant for small adaptation fields (0 and 1.0

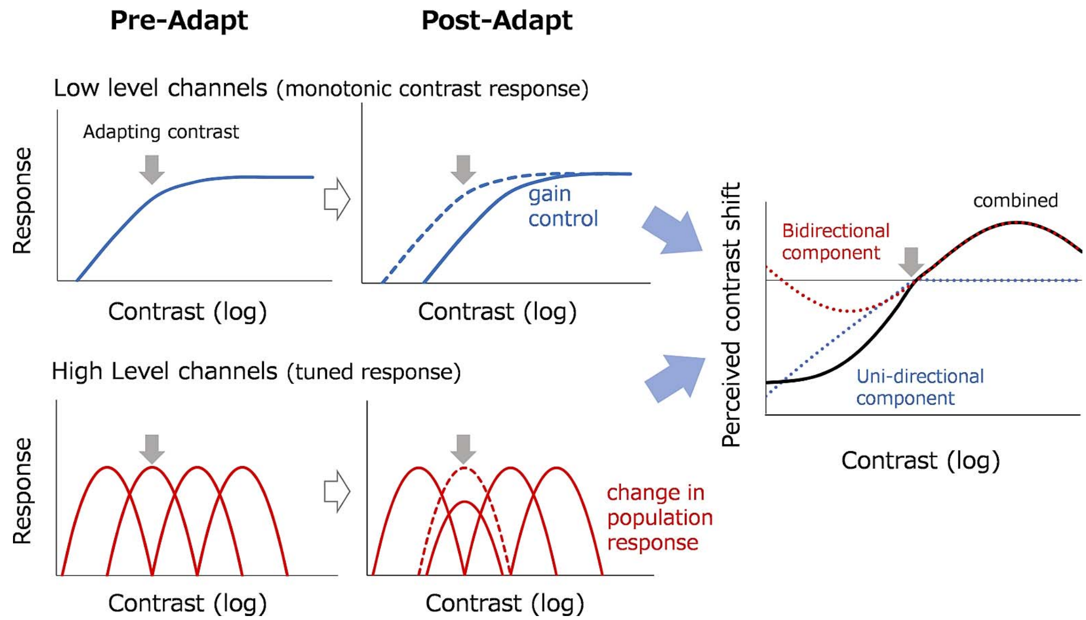

Figure 6. Aftereffects as a result of early contrast gain control and high-level contrast-selective adaptation. Black arrows indicate adaptor contrast. The blue and red curves in the right panel illustrate the low- and high-level components of the aftereffect respectively. The black curve represent the sum of the two.

degrees^2), but this is likely due to the adaptation of early local units that could reduce the perceived contrast to cancel the enhancement. These data also support the idea that adaptation in higher-level mechanisms, which are known to have large receptive fields, is bidirectional or, in other words, that higher-level adaptation can elicit either enhancements or reductions in perceived contrast depending on adaptor contrast.

Generally, repulsive aftereffects are thought to reflect adaptation in neural channels selectively tuned to a particular visual attribute (Blakemore et al., 1973; Blakemore et al., 1970). In the orientation domain, for example, repulsive aftereffects (e.g., tilt aftereffects) can be explained by a population of orientation-selective channels whose peak response to a test stimulus is shifted after a subset of channels have undergone prolonged exposure to an adaptor (Wandell, 1995). By analogy, we suggest that repulsive contrast aftereffects observed in the present study can be interpreted as evidence for neural channels responding selectively to relatively narrow ranges of luminance contrasts. Based on this idea, the curves obtained in our experiment (Figure 2) may be modeled as the sum of two components shown in Figure 6. The first component concerns low-level adaptation in vision's early units. In its pre-adapted state, contrast response increases monotonically with test contrast up to a point of saturation (top left panel in Figure 6). In its post-adapted stated, contrast response is shifted to higher test contrasts (top right panel in Figure 6) as a result of low-level adaptation that effectively turns down input gain. Low-level gain control/adaptation may serve to reposition the contrast-response curve such that its limited dynamic range is optimally reallocated to cover the new higher-contrast regime imposed by the adaptor. The second component concerns higher-level adaptation whereby contrast response is altered in a repulsive manner by reducing sensitivity within a subset of "contrast-selective" units tuned to the adaptor's contrast. Although contrast-selective channels may be equally responsive in their pre-adapted state (bottom left panel of Figure 6), the sensitivity of contrast channels most tuned the adaptor's contrast would be comparatively depressed (bottom right panel of Figure 6). Crucially, as we illustrated, selective reduction in contrast-channel sensitivity accounts for bidirectional contrast after effects. Combining the first (low-level) and second (high-level) adaptive components (right-most panel of Figure 6) provides the necessary asymmetry between perceived contrast reduction and contrast enhancement that we observed empirically.

It is generally argued that units in visual system increase their response monotonically over the entire range of possible image contrasts (Määttänen & Koenderink, 1991; Ohzawa et al., 1982). It may therefore appear unusual to argue for an emseble of channels each selectively tuned to a particular contrast range. However, physiological studies on cortical color processing report neurons in inferotemporal cortex that respond selectively to specific chromatic saturations (e.g., pink, but not red) (Komatsu, Ideura, Kaji, &

Yamane, 1992; Kotake, Morimoto, Okazaki, Fujita, & Tamura, 2009). Such high-level cortical representations presumably reflect further transformations from trichromatic and opponent color representations though multiple levels of processing (Gegenfurtner, 2003) and are thought to underlie "categorical" color perception as revealed by psychophysical studies (Berlin & Kay, 1992; Bornstein & Korda, 1984; Uchikawa & Boynton, 1987). Indeed, in a color study of our own, we found repulsive saturation aftereffects whereby low- and high-saturation stimuli were perceived to have lower and higher saturations respectively after prolonged exposure to an intermediate-saturation adaptor (Mori, 2015). In light of evidence from the color domain, it is not unreasonable to posit similar categorical neural representations for luminance contrast. In a classical study, Snowden and Hammett (1996) have shown that suppressive effects of adaptation on suprathreshold contrast perception exhibit a little broader spatial range than those on threshold contrast detection. This is also consistent with the notion that suprathreshold contrast perception is determined by the both of low-level units with narrow spatial tuning and high-level units with broad spatial tuning.

Results from Experiment 2 show that bidirectional contrast aftereffects are observed only for successive test and reference stimuli. This key methodological innovation likely accounts for the fact that bidirectional aftereffects have not been reported in previous contrast studies in which test and reference stimuli were presented simultaneously. A similar pattern of results has been reported for texture density: Texture density aftereffects are either unidirectional or bidirectional depending on whether test and reference stimuli are presented either simultaneously or successively (Sun & Baker, 2017). It is unclear why the directionality of aftereffects depends critically on the relative timing between test and reference stimuli, but a partial explanation may lie in the fact that different mechanisms are likely involved in successive and simultaneous visual stimulus discrimination. For example, thresholds for discriminating the orientation of two gratings are elevated if stimuli are presented successively (i.e., the oblique effect) but not if they are presented simultaneously (Heeley & Buchanan-Smith, 1992). A different line of evidence shows that after adapting to a texture consisting of elements with different contrast levels, the relative contrasts between elements in the test texture are perceived as shifted away from baseline in a repulsive fashion (straddle illusion: Wolfson & Graham, 2007, 2009). Although the nature of the underlying mechanisms remains uncertain, discrimination between successive stimuli necessarily involves comparisons between memorized stimulus representations whereas discrimination between simultaneous stimuli may recruit more immediate mechanisms (e.g., spatial receptive fields) that could assist in detecting important stimulus differences. Although speculative, this line of reasoning offers at least a partial account of the data in the present study. As our aforementioned model illustrates, bidirectional aftereffects are not expected with simultaneous test and reference stimuli if the perceptual decision hinges on comparing outputs between low-level contrast units with monotonic contrast responses, as would a second-order spatial filter for instance (Landy & Graham, 2004; Graham, 2011; Motoyoshi & Kingdom, 2007). Alternatively, if sucessive test and reference stimuli force the visual system into comparing higher-level repulsive representations stored in working memory, then one might expect bidirectional aftereffects. Naturally, these explanations are conjectural and need to be further tested.

In the psychophysical literature, luminance contrast has traditionally been considered as a low-level image feature, and the perception of contrast has been correspondingly attributed to the response of early visual units. This approach, however, may be misleading. Consider, for instance, that the perception of "red" not only correlates with the low-level response of L cones but also with multiple color-processing levels and neural representations of color in the visual hierarchy (Gegenfurtner, 2003). By analogy, it is sensible that our perception of "high contrast" is also similarly represented within a multistage visual contrast-processing hierarchy. If such is the case, then bidirectional contrast aftereffects would constitute useful tools to analyze high-level quasicategorical neural representations and processing of contrast or lightness. More generally, results from the current study imply that adaptation experiments in which the test and reference stimuli are shown successively may be applied to further investigate high-level neural representations of various visual attributes such as shape, face, and materials.

In all the experiments, perceived contrast enhancement following adaptation was observed for all observers when the contrast of the test stimulus was fourfold of the adaptor and the adaptor was flashed six times or more. The difference between all these data and physical contrast was significant (one-sided t test: $t(43) = 14.1$, $p < 0.0001$). Nevertheless, the effect of perceived contrast enhancement was not extremely strong. In some conditions, perceived contrast enhancement might be limited to a somewhat higher value than contrast discrimination thresholds. As in the present study, experiments in which perception of an observer is examined could be affected by biases. For example, Carrasco et al. (2004) reported that spatial attention altered the appearance of a stimulus, but Schneider and Komlos (2008) have challenged the argument with a conclusion that attention biased the decision but did not alter the appearance of the stimulus (see also Carrasco, 2011). In the present study, we employed a 2AFC, thus the results were not likely to be affected by the bias, which was specified as a decisional bias by Morgan, Melmoth, and Solomon (2013). Since perceived contrast enhancement was not extremely strong, however, it is possible that the results were affected by unknown biases which derived from the experimental procedure. Therefore, a future task is to elaborate an experimental procedure and examine the possibility of biases.

Keywords: adaptation, aftereffects, contrast

Acknowledgments

This study was partially supported by Japan Society for the Promotion of Science KAKENHI grant-in-aid JP15H03461 (IM) and JP15H05916 (IM).

Commercial relationships: none.
Corresponding author: Wakana Hata; Isamu Motoyoshi.
Email: wake.f.m1021@gmail.com; imotoyosi.ac@gmail.com.
Address: Department of Integrated Sciences and Department of Life Science, The University of Tokyo, Tokyo, Japan.

References

Allard, R., & Faubert, J. (2008). The noisy-bit method for digital displays: Converting a 256 luminance resolution into a continuous resolution. *Behavior Research Methods*, *40*(3), 735–743.

Anstis, S., & Ramachandran, V. S. (1987). Visual inertia in apparent motion. *Vision Research*, *27*(5), 755–764.

Berlin, B. & Kay, P. (1992). *Basic color terms: their universality and evolution*. (Revised) Berkeley and Los Angeles, CA: University of California Press.

Blakemore, C., Carpenter, R. H., & Georgeson, M. A. (1970). Lateral inhibition between orientation detectors in the human visual system. *Nature*, *228*(5266), 37–39.

Blakemore, C., Muncey, J. P., & Ridley, R. M. (1973). Stimulus specificity in the human visual system. *Vision Research*, *13*(10), 1915–1931.

Blakemore, C., Nachmias, J., & Sutton, P. (1970). The perceived spatial frequency shift: Evidence for frequency-selective neurones in the human brain. *The Journal of Physiology*, *210*(3), 727–750.

Blakemore, C., & Sutton, P. (1969). Size adaptation: A new aftereffect. *Science*, *166*(3902), 245–247.

Bornstein, M. H., & Korda, N. O. (1984). Discrimination and matching within and between hues measured by reaction times: Some implications for categorical perception and levels of information processing. *Psychological Research*, *46*(3), 207–222.

Carrasco, M. (2011). Visual attention: The past 25 years. *Vision Research*, *51*(13), 1484–1525.

Carrasco, M., Ling, S., & Read, S. (2004). Attention alters appearance. *Nature Neuroscience*, *7*(3), 308–313.

Carrasco, M., Penpeci-Talgar, C., & Eckstein, M. (2000). Spatial covert attention increases contrast sensitivity across the CSF: Support for signal enhancement. *Vision Research*, *40*(10-12), 1203–1215.

Durgin, F. H. (1995). Texture density adaptation and the perceived numerosity and distribution of texture. *Journal of Experimental Psychology: Human Perception and Performance*, *21*(1), 149.

Durgin, F. H., & Huk, A. C. (1997). Texture density aftereffects in the perception of artificial and natural textures. *Vision Research*, *37*(23), 3273–3282.

Durgin, F. H., & Proffit, D. R. (1996). Visual learning in the perception of texture: Simple and contingent aftereffects of texture density. *Spatial Vision*, *9*(4), 423–474.

Gegenfurtner, K. R. (2003). Cortical mechanisms of colour vision. *Nature Reviews Neuroscience*, *4*(7), 563–572.

Georgeson, M. A. (1985). The effect of spatial adaptation on perceived contrast. *Spatial Vision*, *1*(2), 103–112.

Gibson, J. J. & Radner, M. (1937). Adaptation, after-effect and contrast in the perception of tilted lines. I. Quantitative studies. *Journal of Experimental Psychology*, *20*, 453–467.

Gilbert, C. D., & Wiesel, T. N. (1990). The influence of contextual stimuli on the orientation selectivity of cells in primary visual cortex of the cat. *Vision Research*, *30*(11), 1689–1701.

Graham, N. V. (2011). Beyond multiple pattern analyzers modeled as linear filters (as classical V1 simple cells): Useful additions of the last 25 years. *Vision Research*, *51*(13), 1397–1430.

Greenlee, M. W., Georgeson, M. A., Magnussen, S., & Harris, J. P. (1991). The time course of adaptation to spatial contrast. *Vision Research*, *31*(2), 223–236.

Hammett, S. T., Snowden, R. J., & Smith, A. T. (1994).

Perceived contrast as a function of adaptation duration. *Vision Research*, *34*(1), 31–40.

Heeley, D. W., & Buchanan-Smith, H. M. (1992). Orientation acuity estimated with simultaneous and successive procedures. *Spatial Vision*, *6*(1), 1–10.

Heron, J., Aaen-Stockdale, C., Hotchkiss, J., Roach, N. W., McGraw, P. V., & Whitaker, D. (2012). Duration channels mediate human time perception. *Proceedings of the Royal Society B*, *279*(1729), 690–698.

Komatsu, H., Ideura, Y., Kaji, S., & Yamane, S. (1992). Color selectivity of neurons in the inferior temporal cortex of the awake macaque monkey. *Journal of Neuroscience*, *12*(2), 408–424.

Kotake, Y., Morimoto, H., Okazaki, Y., Fujita, I., & Tamura, H. (2009). Organization of color-selective neurons in macaque visual area V4. *Journal of Neurophysiology*, *102*(1), 15–27.

Landy, M. S., & Graham, N. (2004). Visual perception of texture. *The Visual Neurosciences*, *1*, 1106–1118.

Levinson, E., & Sekuler, R. (1976). Adaptation alters perceived direction of motion. *Vision Research*, *16*(7): 779–781.

Määttänen, L. M., & Koenderink, J. J. (1991). Contrast adaptation and contrast gain control. *Experimental Brain Research*, *87*(1), 205–212.

Morgan, M. J., Melmoth, D., & Solomon, J. A. (2013). Linking hypotheses underlying Class A and Class B methods. *Visual Neuroscience*, *30*(5-6), 197–206.

Mori, S. (2015). Psychophysical analyses of high-level color repretations in the human visual system: An adaptation study. Graduation thesis at the Department of Integrated Sciences, The University of Tokyo (in Japanese).

Motoyoshi, I & Kingdom, F. A. (2007). Differential roles of contrast polarity reveal two streams of second-order visual processing. *Vision Research*, *47*(15), 2047–2054.

Movshon, J. A., & Lennie, P. (1979). Pattern-selective adaptation in visual cortical neurones. *Nature*, *278*(5707), 850–852.

Ohzawa, I., Sclar, G., & Freeman, R. D. (1982). Contrast gain control in the cat visual cortex. *Nature*, *298*(5871), 266–268.

Ramachandran, V. S., & Anstis, S. M. (1983). Extrapolation of motion path in human visual perception. *Vision Research*, *23*(1), 83–85.

Regan, D., & Hamstra, S. J. (1992). Shape discrimination and the judgement of perfect symmetry: Dissociation of shape from size. *Vision Research*, *32*(10), 1845–1864.

Ross, J., & Speed, H. D. (1996). Perceived contrast following adaptation to gratings of different orientations. *Vision Research*, *36*(12), 1811–1818.

Sato, H., Motoyoshi, I., & Sato, T. (2016). On-off selectivity and asymmetry in apparent contrast: An adaptation study. *Journal of Vision*, *16*(1):14, 1–11, https://doi.org/10.1167/16.1.14. [PubMed] [Article]

Schneider, K. A., & Komlos, M. (2008). Attention biases decisions but does not alter appearance. *Journal of Vision*, *8*(15):3, 1–10, https://doi.org/10.1167/8.15.3. [PubMed] [Article]

Sclar, G., Lennie, P., & DePriest, D. D. (1989). Contrast adaptation in striate cortex of macaque. *Vision Research*, *29*(7), 747–755.

Smith, A. T., Singh, K. D., Williams, A. L., & Greenlee, M. W. (2001). Estimating receptive field size from fMRI data in human striate and extrastriate visual cortex. *Cerebral Cortex*, *11*(12), 1182–1190.

Snowden, R. J., & Hammett, S. T. (1996). Spatial frequency adaptation: Threshold elevation and perceived contrast. *Vision Research*, *36*(12), 1797–1809.

Sun, H. C., & Baker, C. L. (2017). Texture density adaptation can be bidirectional. *Journal of Vision*, *17*(8):9, 1–10, https://doi.org/10.1167/17.8.9. [PubMed] [Article]

Suzuki, S., & Cavanagh, P. (1998). A shape-contrast effect for briefly presented stimuli. *Journal of Experimental Psychology: Human Perception and Performance*, *24*(5), 1315–1341.

Uchikawa, K., & Boynton, R. M. (1987). Categorical color perception of Japanese observers: Comparison with that of Americans. *Vision Research*, *27*(10), 1825–1833.

Wandell, B. A. (1995). *Foundations of vision*. Sunderland, MA: Sinauer Associates.

Webster, M. A., Kaping, D., Mizokami, Y., & Duhamel, P. (2004). Adaptation to natural facial categories. *Nature*, *428*(6982), 557–561.

Webster, M. A., & Maclin, O. H. (1999). Figural aftereffects in the perception of faces. *Psychonomic Bulletin & Review*, *6*(4), 647–653.

Webster, M. A. & Mollon, J. D. (1991, January 17). Changes in color appearance following post-receptoral adaptation. *Nature*, *349*(17), 135–137.

Wilson, H. R., & Humanski, R. (1993). Spatial frequency adaptation and contrast gain control. *Vision Research*, *33*(8), 1133–1149.

Wolfson, S. S., & Graham, N. (2007). An unusual kind of contrast adaptation: Shifting a contrast comparison level. *Journal of Vision*, *7*(8):12, 1–7, https://doi.org/10.1167/7.8.12. [PubMed] [Article]

Wolfson, S. S., & Graham, N. (2009). Two contrast adaptation processes: Contrast normalization and shifting, rectifying contrast comparison. *Journal of Vision*, *9*(4):30, 1–23, https://doi.org/10.1167/9.4.30. [PubMed] [Article]

Yoshikawa, S., & Sato, W. (2008). Dynamic facial expressions of emotion induce representational momentum. *Cognitive, Affective, & Behavioral Neuroscience*, *8*(1), 25–31.

Zeki, S. M. (1978). Uniformity and diversity of structure and function in rhesus monkey prestriate visual cortex. *The Journal of Physiology*, *277*(1), 273–290.