Brief presentation enhances various simultaneous contrast effects

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Kaneko and Murakami (2012) demonstrated that simultaneous contrast for brightness and color (chromatic saturation) were enhanced by flashing the stimulus very briefly (10 ms). Here we examined whether this effect of duration generalized to other visual features. Tilt illusion and simultaneous hue contrast were both shown to be much stronger with a stimulus duration of 10 ms compared with 500 ms. The similar temporal dynamics for simultaneous contrast across visual features suggest common underlying principles.

Introduction

The appearance of a stimulus is dependent upon what surrounds it. Spatial context is known to change how a stimulus appears in many different ways. Simultaneous contrast is one such phenomenon. If a gray patch is surrounded by black or white, it appears lighter or dimmer, respectively (simultaneous brightness contrast; e.g., Heinemann, 1955). If the surround is colored, such as green or red, it appears to be tinted with its surround's complementary colors, i.e., reddish or greenish, respectively (simultaneous color contrast).

The temporal characteristics of these spatial context effects had been widely considered "slow" (for example, De Valois, Webster, De Valois, & Lingelbach, 1986). However, more recent studies indicate otherwise (Blakeslee & McCourt, 2008; Kaneko & Murakami, 2012; Robinson & de Sa, 2008). In our previous study

(Kaneko & Murakami, 2012), we examined the temporal dynamics of the simultaneous contrast of brightness and color (chromatic saturation). We found that both effects were much enhanced (in most cases more than doubled) at 10 ms duration compared with 500 ms duration. Furthermore, the strength of the illusions decreased rapidly with increasing stimulus duration, reaching a plateau at around 100 ms (Kaneko & Murakami, 2012, experiments 4 and 5). To be aligned with the literature, we suggest two mechanisms: one fast and one slow. The fast simultaneous contrast process is rapid enough to respond to 10 ms stimulus and yields strong simultaneous contrast effects. The other simultaneous contrast process is slow but produces just moderate amounts of illusion.

Simultaneous contrast has been found for many visual features, not just brightness and color. Among such features are orientation/tilt (Blakemore, Carpenter, & Georgeson, 1970; Gibson, 1937; Westheimer, 1990), spatial frequency/size (Klein, Stromeyer, & Ganz, 1974), depth (Graham & Rogers, 1982), luminance contrast (Chubb, Sperling, & Solomon, 1989), chromatic saturation/contrast (Brown & MacLeod, 1997), motion (S. Anstis & Casco, 2006; Duncker, 1929/1938), blur (M. A. Webster, Georgeson, & Webster, 2002; S. M. Webster, Webster, Taylor, Jaikumar, & Verma, 2001), and so on. We have shown the duration effect on brightness and color (chromatic saturation) versions of simultaneous contrast in Kaneko and Murakami (2012), but are other simultaneous contrast effects also enhanced by briefly flashing the stimulus?

We focused on the tilt illusion and on the simultaneous hue-contrast effect using unique yellow. We found a similar relationship between the stimulus duration and the illusion strength, which suggests a common principle across visual features.

Experiment 1: Brief exposure enhances the tilt illusion multiplicatively

The perceived orientation of a stimulus (grating or a single line) is affected by the orientation of a surrounding stimulus (again grating or lines). In Gibson's (1937) "direct effect," the center stimulus seems tilted *away* from the surrounding stimulus when the orientation difference between the center and surround is relatively small (<40°–45°) whereas in the "indirect effect" it seems slightly tilted *toward* the surrounding stimulus when the orientation difference is large (60°–80°; Blakemore et al., 1970; Gibson, 1937). We focus only on the direct effect in which the surround orientation differs from the target by <45°. The strength of the tilt illusion depends on this orientation difference and is known to peak at an orientation difference of 15°–20° (Blakemore et al., 1970; Over, Broerse, & Crassini, 1972; Westheimer, 1990).

The previous studies seem to disagree as to the effect of duration on the tilt illusion. Calvert and Harris (1988) claimed the tilt illusion was strongest when the duration was about 100 ms and decreased as the duration became shorter than that. Similarly, B. I. O'Toole (1979), using a test line with inducing gratings, showed that the tilt illusion effect increased as the duration increased from 10 ms up to 1000 ms. On the other hand, Wenderoth and his colleagues (Wenderoth & Johnstone, 1988; Wenderoth & van der Zwan, 1989) showed that the strength of the illusion was strongest at the shortest duration they tested (10 ms) and decreased as the duration became longer, coming down to a plateau at around 100 ms. Westheimer (1990) generally agreed with these results. One of the purposes of this experiment was to help resolve this contradiction.

All of these abovementioned studies on stimulus duration used only a 15° orientation difference with a vertical target, which was apparently designed to maximize the tilt illusion strength. Because of this experimental design, we could not tell how the orientation difference affected the tilt illusion as a function of the duration. For the "normal" tilt illusion, the function is an inverted U, peaking at 15°–20° as was mentioned. Does decreasing the duration change the shape of this curve, and if so, in what way? One

possible change of the illusion is additive; that is, a constant amount of illusion might always be added when the duration is short. Thus, the illusion might increase by, say, 5° regardless of the original illusion strength with long exposure. Another possible change is multiplicative: The illusion is always increased by the same factor. To answer this question, we varied the orientation difference between the target and the surrounding grating over a wide range.

These potential forms of increase have different implications. If short durations increase the illusion additively, this implies an additional mechanism that only works when the duration is short and creates an extra illusory tilt in addition to the one created by the other mechanism. A multiplicative increase would imply an increased gain in a single mechanism.

Method

Observers

Six observers participated in this experiment. All observers had normal or corrected-to-normal visual acuity. All experiments in this research were conducted in accord with the Code of Ethics of the World Medical Association (Declaration of Helsinki). Observers gave an informed and written consent to the participation. They were unaware of the purpose of the study.

Apparatus

All stimuli were presented on a 19-in. CRT monitor (SONY CPD-G400; Sony Corporation, Tokyo, Japan; 1280 × 960 pixels, refresh rate 100 Hz, graphic card ATI Radeon HD 5770 1024 MB) controlled by an Apple MacPro (Apple, Inc., CA). Viewing distance was 52 cm (binocular viewing). A chin rest was used to maintain the viewing distance. The experiment was run in a darkened room.

Stimulus

All stimuli were generated using the MATLAB (The MathWorks, MA) programming environment with Psychtoolbox (Brainard, 1997; Pelli, 1997) routines. The test stimulus whose orientation was to be judged was a sinusoidal grating with a hard-edged circular window (3° diameter). It was embedded at the center of a larger disk filled with a sinusoidal grating (8° diameter, the surround). Both grayscale gratings had a spatial frequency of 2 c/° and a luminance contrast of 100%. The test grating was always vertical (=0° hereafter). To aid the visibility of the test grating, the relative spatial phase difference between the test grating and the surrounding grating was always fixed at 1/4 pi (45°) although the absolute spatial phase was chosen

randomly for each trial. Orientations of the surround were varied from 3° to 19° with a 2° step, both clockwise and counterclockwise, resulting in 18 conditions. The comparison grating was identical to the test grating except that its orientation was adjustable. The rest of the display was mean-luminance gray (32 cd/m^2). Test grating and comparison grating were presented side by side with a 10° center-to-center distance between them. Their right/left positions were randomized across sessions. No fixation point was provided, and the observers were encouraged to move their eyes to make their judgments. To avoid any possible effect of the display edge on the orientation judgment, the whole display was covered with matte black paper with an oval window (approximately 36° × 25°).

Procedure

An adjustment method was used in this experiment. During a trial, the test and the surround were repeatedly presented on one side or the other of the display with a 500-ms blank interval in between. Duration of the test and the surround was either 10 ms (flashed condition) or 500 ms (steady condition). During the blank, a uniform gray field replaced the test and the surround. The observers' task was to adjust the orientation of the comparison grating, which was presented on the other side of the fixation point, using the assigned keys to make it look parallel to the test grating. The comparison grating was always visible to the observer throughout the trial. The initial orientation of the comparison grating was randomly preset between −45° and +45° for each trial. There was no time restriction on making the adjustment. Once the observer was satisfied with the adjustment, he or she pressed the space key to initiate the next trial. During the 2-s intertrial intervals, a static black-and-white noise pattern was presented to eliminate any afterimages. All (18 surround × 2 duration) conditions were run in one session in randomized order. Four adjustments were made per condition per observer.

Results and discussion

Data from the clockwise and counterclockwise conditions were merged for further analyses. This way, any perceptual or judgmental bias to the vertical was lost. The difference between the matched comparison grating's orientation and the physical orientation of the test grating (=0°) was defined as the tilt illusion. It was positive if the test looked tilted away from the surround orientation and negative if the test looked tilted toward the surround orientation, which was rare.
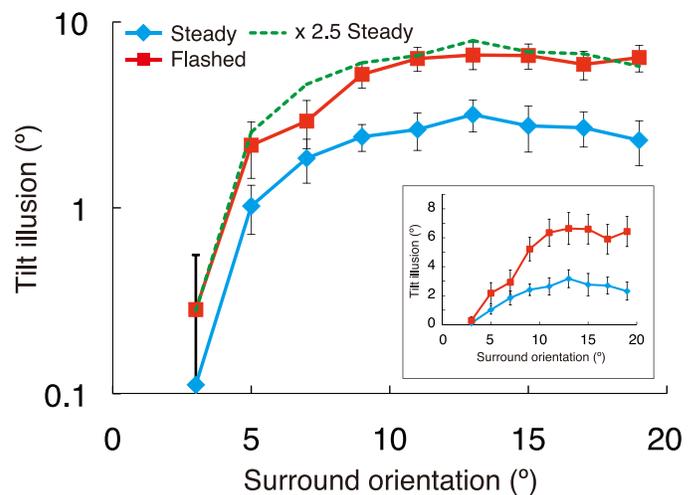

Figure 1. Results of Experiment 1. Subjective tilt of the physically vertical test grating with various surround gratings. Mean ±1 *SE* of six observers. Note that the vertical axis is logarithmic (the inset shows the same data with a linear vertical axis). Blue diamonds are for the steady condition and red squares for the flashed condition. Green dotted line represents the steady condition data × 2.5.

The surround orientation could take one of nine values varying from 3° to 19°. Figure 1 shows the mean tilt illusion obtained in Experiment 1. Note that the vertical axis is logarithmic. For all surround orientation conditions, we found that flashed conditions (red square symbols) always produced a greater effect than steady conditions (blue diamond symbols). Two-way ANOVA showed significant interaction (surround orientation × duration), $F(8, 40) = 14.5$, $p < 0.05$, as well as significant main effects of surround orientation, $F(8, 40) = 20.6$, $p < 0.05$, and duration, $F(1, 5) = 45.4$, $p < 0.05$. The interaction term possibly came from the flatter (on linear scale, see the inset of Figure 1) curve of the steady condition rather than that of the flashed condition; analysis of interaction showed that for the steady condition significant differences were found only between 3° and conditions >7° and between 5° and 13° whereas for the flashed condition significant differences were found between 3° and >5°, 5° and >9°, and 7° and >9°. Furthermore, analysis of interaction showed that there were significant differences between the flashed and steady conditions at all orientation conditions except 3° ($p < 0.05$).

Tilt illusions for the steady condition lay along unimodal curves peaking at 13°, which was in line with the literature (i.e., Blakemore et al., 1970; B. O'Toole & Wenderoth, 1977; Westheimer, 1990). This is also true for the red curve (flashed condition). The new dotted green curve shows that the steady condition data multiplied by 2.5 coincide with the red curve. This shows that regardless of the surround orientation conditions, the tilt illusion for the flashed condition was

always approximately 2.5 times the steady condition illusion. For surround orientations greater than ~11°, the tilt illusion reached plateaus of approximately 6.4° in flashed conditions and 2.7° in steady conditions.

Experiment 2: Simultaneous hue contrast

Simultaneous *color* contrast can take two forms, depending on the test patch. A red or green surround will make a *gray* test patch look greenish or pinkish, thus shifting its apparent *saturation*. The same surrounds will make a *yellow* test patch look lime or orange, thus shifting its apparent *hue*. We shall call these saturation-shift and hue-shift simultaneous contrast, respectively. In Experiment 2, we explored the parallelism between simultaneous contrast in orientation and color (hue) dimensions by looking for the effects of short durations upon inductions of tilt and hue.

Studies of postopponent color mechanisms pointed out the presence of narrowly tuned neurons in the primate visual cortex, each of which is selective to hues lying in intermediate directions between the cardinal axes in cone-opponent color space. Electrophysiological studies in the primary visual cortex (V1) of the macaque (Hanazawa, Komatsu, & Murakami, 2000; Lennie, Krauskopf, & Sclar, 1990; Wachtler, Sejnowski, & Albright, 2003) have revealed the presence of mechanisms selective to intermediate hues. A recent fMRI study reported that the same is true in humans (Kuriki, Sun, Ueno, Tanaka, & Cheng, 2015). Along with these studies, a recent psychophysical study (Klauke & Wachtler, 2015) made an attempt to draw a parallel between the mechanisms of orientation selectivity and hue selectivity using simultaneous hue contrast.

The orientation selectivity of neurons in macaque V1 is known to take several tens of milliseconds to build up (Ringach, Hawken, & Shapley, 1997, 2003). The difference in orientation contrast effect with stimulus duration (Experiment 1) could be related to such a property of cortical neurons. According to another study, hue-tuning properties of macaque V1 neurons vary in time within 100 ms after stimulus onset (Cottaris & DeValois, 1998), suggesting that hue-tuning mechanisms could also follow similar buildup process to the orientation-selective ones (Ringach et al., 1997, 2003). On the contrary, a psychophysical study in human subjects, measuring color categorization and color discriminations in *hue* direction, claimed that no significant difference was found for 50 ms stimulus presentation compared with 500 ms (Cropper, Kvansakul, & Little, 2013).

Considering the possible parallelism between the orientation- and hue-selective mechanisms and the presence of enhanced simultaneous *saturation* contrast (Kaneko & Murakami, 2012), in addition to the result of Experiment 1, the similar effect of stimulus duration may exist in simultaneous *hue*-contrast effects. In addition, confirmation of the contrast-enhancement effect for *hue* in a short period may give some hint to solve the controversy among physiological and psychophysical studies (Cottaris & DeValois, 1998; Cropper et al., 2013). Therefore, we tested the enhancement of the simultaneous hue-contrast effect due to a short stimulus presentation.

As a target color in this experiment, we used unique yellow. Unique hues are perceptually pure colors that do not seem to be tinted with any other color (De Valois, De Valois, Switkes, & Mahon, 1997; M. A. Webster, Miyahara, Malkoc, & Raker, 2000). The value of unique yellow, which does not look reddish or greenish, is slightly different, but stable, for each individual observer.

Unique yellow and the vertical orientation share an important feature: Observers can judge whether a stimulus is yellow or not, or vertical or not, without a comparison. This feature is particularly important in the experiment on color appearance, considering the possibility of drift in the state of chromatic adaptation during the matching procedure; an observer's visual system may adapt to two different surrounds alternatively and frequently, which may lead to an unstable or undefined state of chromatic adaptation. The other possibility of bias or offset can be considered if asymmetric color matching is conducted by adjusting the color of a comparison patch in, e.g., a neutral background; differences in background color usually do not yield satisfactory match in appearance. Therefore, the unique yellow enabled us to use the nulling method with a single stimulus presentation to measure the strength of the hue-shift type of simultaneous contrast in this experiment.

Method

Observers

Five observers participated in this experiment. All of these five participated in Experiment 1 as well. All had normal or corrected-to-normal visual acuity and normal color perception as tested with the standard Ishihara color test.

Apparatus

Experiments 1 and 2 used the same apparatus. We calibrated the CRT screen chromaticity using our original measurements and a conventional method of
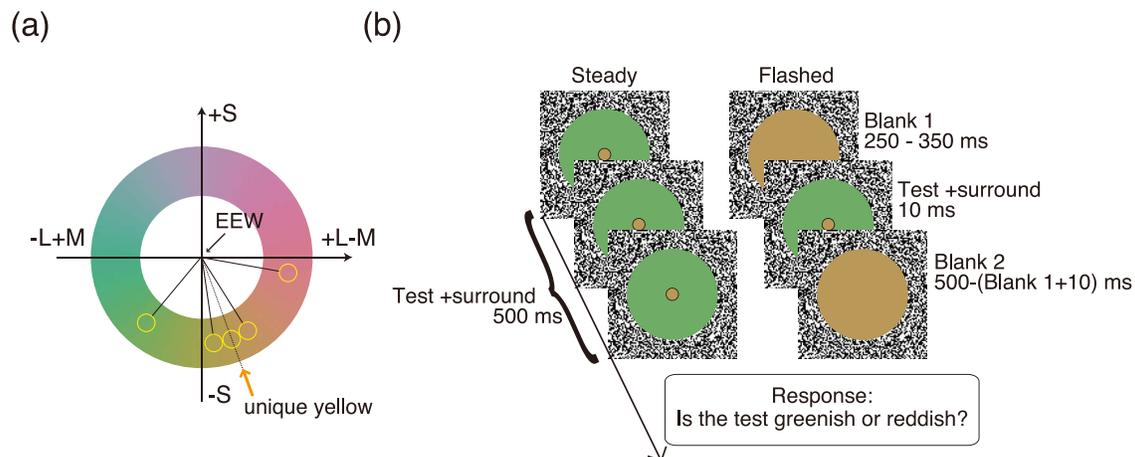
Figure 2. (a) Representation of color space used in Experiment 2. The origin of the color space was equal energy white at 20 cd/m². All the colors are equiluminant and defined by azimuth. Five surround color conditions (yellow circles) were chosen relative to each observer's original unique yellow. (b) Schematic description of a trial in Experiment 2. The test and the surround were presented simultaneously for either 10 ms (flashed) or 500 ms (steady). In the flashed condition, the surround area was filled with the observer's original unique yellow before and after the test presentation. After the stimulus disappeared, the observer responded whether the test appeared greenish or reddish.

linearization of luminance in each color primary (see Cowan, 1983, and appendix A of Horiuchi, Kuriki, Tokunaga, Matsumiya, & Shioiri, 2014).

Stimulus

All stimuli were generated using the MATLAB (MathWorks) programming environment with Psychtoolbox (Brainard, 1997; Pelli, 1997) routines. All the colors used in this experiment were chosen from an equiluminant cone-opponent color ring whose center was the equal energy white ([X, Y, Z] = [20, 20, 20] in CIE tristimulus values; Figure 2a). Hues are indicated by azimuth on the hue circle with 0° being +L − M "red," +90° being +S "lavender," +180° being −L + M "green," and +270° being −S "lime." Saturations of these hues were fixed throughout the experiment. Amplitude of the L − M modulation was 7% in L-cone contrast of the equal energy white, and the amplitude of the S modulation was 70% in S-cone contrast of the equal energy white, which approximately equates the apparent chromatic saturation between the L − M and S axes. These values were determined based on the color gamut limitation of our monitor.

The test stimulus was a uniformly colored disk (diameter = 1°) embedded in a uniformly colored larger disk (diameter 8°). The test had a thin black contour to ensure its visibility (cf. Kaneko & Murakami, 2012). The hue of the larger disk (surround hue, hereafter) was determined relative to each observer's original unique yellow (=0°). Surround hue conditions were ±12°, 60°, and 0° in hue angle (here positive sign means a counterclockwise shift on the hue circle). The observer's responses drove the test hue along a staircase. The

rest of the display was filled with a static luminance noise pattern (Figure 2b).

Procedure

Equiluminance of the hue circle was ensured by performing heterochromatic flicker photometry for each observer before running the main experiment. Furthermore, each observer's unique yellow was determined by a two-alternative forced choice in a preliminary experiment. A disk (8° diameter) filled with uniform color was presented for 500 ms. An observer viewed it foveally and determined whether the color appeared either "greenish" or "reddish." Chromaticity of the disk was adjusted per trial with a staircase method with a step of 3.75°, and the last four reversal points were averaged to yield the session's response. The average of four staircases was determined as an "original" unique yellow for the observer. Azimuth data of all observers' "original" unique yellow are shown in Table 1. The average unique yellow azimuth angle was 294°, which was comparable to previous literatures (e.g., De Valois et al., 1997; M. A. Webster et al., 2000).

Observers	"Original" unique yellow (azimuth, [°])
O1	285.7
O2	292.0
O3	307.0
O4	292.3
O5	290.9
Average (SD)	293.6 (7.1)

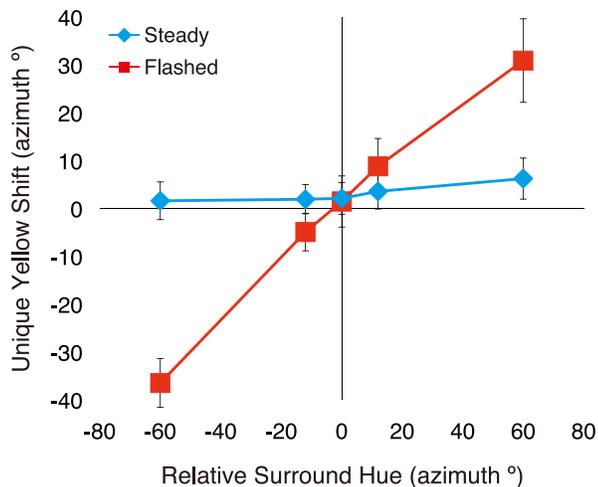Table 1. "Original" unique yellow of all the observers.

Figure 3. Results of Experiment 2. Mean ±1 *SE* hue shift of unique yellow ($N = 5$). On both vertical and horizontal scales, zero is normalized to each observer's "original" unique yellow. The positive *x* values represent the physical shift of the surround toward red, and the negative values represent shift toward green. The positive *y* values represent the *perceptual* shift of unique yellow toward green, and the negative values represent shift toward red. Thus, a red surround makes unique yellow look greenish and vice versa.

Test and surround were presented simultaneously at the center of the display. The observer's task was to determine whether the test hue appeared either greenish or reddish (Figure 2b). No instruction or reference was given as to the definitions of "green" or "red." Test and surround duration was either 10 ms (flashed) or 500 ms (steady). For the flashed condition, before and after the presentation of the stimulus, there were blank periods. During these, the surround and the test area were filled with "original" unique yellow to compensate for the duration difference. Onset of the test presentation was randomly determined trial by trial to begin between 250 and 350 ms after the first blank field. The total duration of three phases, i.e., the first blank, the test plus surround, and the second blank, was 500 ms. The test hue was varied according to a one-up, one-down staircase to determine the "new" (postcontrast) unique yellow for each condition. Five surround hue conditions were run in the same session, and two staircases were run per condition. Flashed and steady conditions were run in separate sessions. Each staircase was terminated after eight reversals. The average of last four reversals was taken as the unique yellow for that condition. The final step size of the staircases was 3.75° (azimuth).

Results and discussion

Figure 3 shows the main result from the nulling experiment. Strength of hue shift type simultaneous contrast was defined as the difference between the "new" unique yellow with various surround hues and the "original" unique yellow. Because we used a nulling method, if the surround hue shifted the test hue away from it (for example, red pushing the test hue into the greenish direction), the "new" unique yellow should be closer to the surround hue than the "original" unique yellow (for example, shifted in the reddish direction).

Overall, "new" unique yellows shifted toward the surround hue direction more for the flashed conditions than for the steady conditions at all surround hues (Figure 3), indicating a stronger effect for the flashed conditions in general. A two-way ANOVA (duration × surround hue) showed significant interaction, $F(4, 16) = 62.4$, $p < 0.05$, as well as a significant main effect of surround hue, $F(4, 16) = 129$, $p < 0.05$, but not duration, $F(1, 4) = 0.39$, $p > 0.05$. Analysis of the interaction revealed that there were significantly larger shifts for the flashed condition than for the steady condition at +60° and −60° conditions, $F(1, 20) = 19.1$, $F(1, 20) = 45.5$, respectively (both ps < 0.05). When linear regression lines were fitted to the data for the two conditions, the slope for the flashed condition was 0.56 whereas the slope for the steady condition was 0.04. In other words, an approximately 14 times bigger shift was found for the flashed than for the steady condition.

For the flashed conditions, the unique yellow shift was as great as an ∼40° shift in hue (−60° condition). These are much stronger effects than previously known effects (cf. Klauke & Wachtler, 2015) and are also larger than our steady conditions. This shows that briefly flashing the stimulus enhances the hue-shift as well as the saturation-shift type of simultaneous contrasts.

Steady conditions gave only small (∼4°) shifts of unique yellow compared with Klauke and Wachtler's (2015) finding of a ∼20° shift at peak. In fact, ANOVA showed *no* significant effect of our steady surround hues, $F(4, 32) = 1.08$, $p > 0.05$. This discrepancy could be partly because of the black outline we used to aid the visibility of the test because the spatial gap had been known to reduce simultaneous contrast (Brenner & Cornelissen, 1991; Oyama & Hsia, 1966; Walraven, 1973). The difference may also be due to differences in methods; Klauke and Wachtler used adjustment, and we used the nulling method.

General discussion

We have demonstrated that the enhancement produced by briefly flashing a simultaneous contrast stimulus, as previously found for brightness and color (saturation-shift type; Kaneko & Murakami, 2012), was also found in the tilt illusion (Experiment 1) and

hue-shift type simultaneous color contrast using unique yellow (Experiment 2).

Data from our Experiment 1 were consistent with Wenderoth's data (Wenderoth & Johnstone, 1988; Wenderoth & van der Zwan, 1989) but not with Calvert and Harris (1988) or B. I. O'Toole (1979), who found a positive relationship between the stimulus duration and the tilt illusion strength (longer durations gave stronger illusions). Our experiment further expanded Wenderoth and Johnstone (1988) and Wenderoth and van der Zwan (1989). By systematically varying the surround orientation, we successfully showed that flashing the stimulus increased the strength of the tilt illusion multiplicatively. Multiplicative increase, rather than additive or otherwise, suggests a common mechanism with a gain change. Thus, we propose that a single mechanism is solely responsible both for the "normal" tilt illusion and also for the much stronger flashed tilt illusion.

Mechanism of the tilt illusion

It is generally accepted that lateral inhibition among orientation-selective units is responsible for the tilt illusion. Blakemore et al. (1970) suggested that orientation-selective units (or cells) with similar orientation selectivity inhibited each other, and so nearby oriented lines induced a perceived tilt into a test line. Blakemore and Tobin (1972) went on to show directly the existence of such lateral interactions among cells in cat's area 17/18; a cell's response to an oriented line is strongly influenced by the presence of other oriented lines even when these surrounding lines are outside the cell's classical receptive field (cRF). A cell's response was suppressed when the surrounding lines were oriented similarly to the line in cRF and was facilitated when the surrounding lines were oriented far apart from the line in cRF. Many authors have since confirmed such effects from oriented lines outside the cRF (e.g., Knierim & Van Essen, 1992; Li, Thier, & Wehrhahn, 2000). Gilbert and Wiesel (1990) showed that surrounding lines could also induce orientation tuning shift and broadening of tuning curves. These were considered to be the neural basis of the tilt illusion (Gilbert & Wiesel, 1990).

These studies support a multiple-channel model of orientation perception based upon a distribution of population responses (Blakemore et al., 1970; Gilbert & Wiesel, 1990). Each individual neuron that is tuned to a certain orientation acts as a "labeled line," and the distribution of responses from a group of multiple labeled lines, each tuned to slightly different orientations, determine the perceived orientation (Gilbert & Wiesel, 1990). Therefore, lateral interactions between these lines, or neurons, can skew the distribution and

change the perceived orientation. Gilbert and Wiesel (1990) described several versions of the multiple-channel model, and some of them replicated the psychophysical data (cf. Blakemore et al., 1970; Westheimer, 1990).

Known psychophysical features of the tilt illusion, such as spatial frequency selectivity (Georgeson, 1973) or partial color selectivity (Clifford, Pearson, Forte, & Spehar, 2003; Clifford, Spehar, Solomon, Martin, & Zaidi, 2003) also suggest low-level locus of the tilt illusion. Taken together, V1 is a likely locus for the main site of the tilt illusion.

Mechanism of the simultaneous hue shift: "'Tilt' in color space" (Klauke & Wachtler, 2015)

The neural foundation of color perception seems more complicated than orientation perception. Color perception starts at the retina with three types of cones tuned to different wavelengths. Neurons in the lateral geniculate nucleus (LGN) are shown to be narrowly selective to colors on so-called cardinal axes (Derrington, Klauskopf, & Lennie, 1984; Hanazawa et al., 2000), and responsiveness to whole arrays of colors seem to start at the level of V1, where scattered selectivity to different hues, including noncardinal hues, were found (e.g., Hanazawa et al., 2000; Kuriki et al., 2015; Wachtler et al., 2003).

For a long time, the neural basis for the color induction was considered to reside in double-opponent color cells (e.g., Lennie, 1999). An ideal double-opponent cell has a receptive field with a concentric center–surround structure, and each area receives opponent signals from different cone types (such as R–/G+ center and R+/G– surround)—and such cells have been found in V1 (Conway, 2001; Livingstone & Hubel, 1984; reviewed by Shapley & Hawken, 2011). Although double-opponent cells can account for color contrast effects toward opponent colors, color contrast effect in *hue* direction cannot be explained with double-opponent cells only. Wachtler et al. (2003) found the contextual effect from the surrounding area on color-selective cells in monkey V1 equivalent to the ones found with orientation. They found that the responses of hue-selective cells in V1 were suppressed in the presence of similar hues lying outside the cRFs and, less often, enhanced by the presence of complementary hues. These responses were consistent with human psychophysical data. Therefore, multiple channel mechanisms, similar to orientation-selective mechanisms, each of which is selective to slightly different hues with mutual suppressions followed by a population coding system, could be the possible neural basis for the simultaneous hue contrast effect.
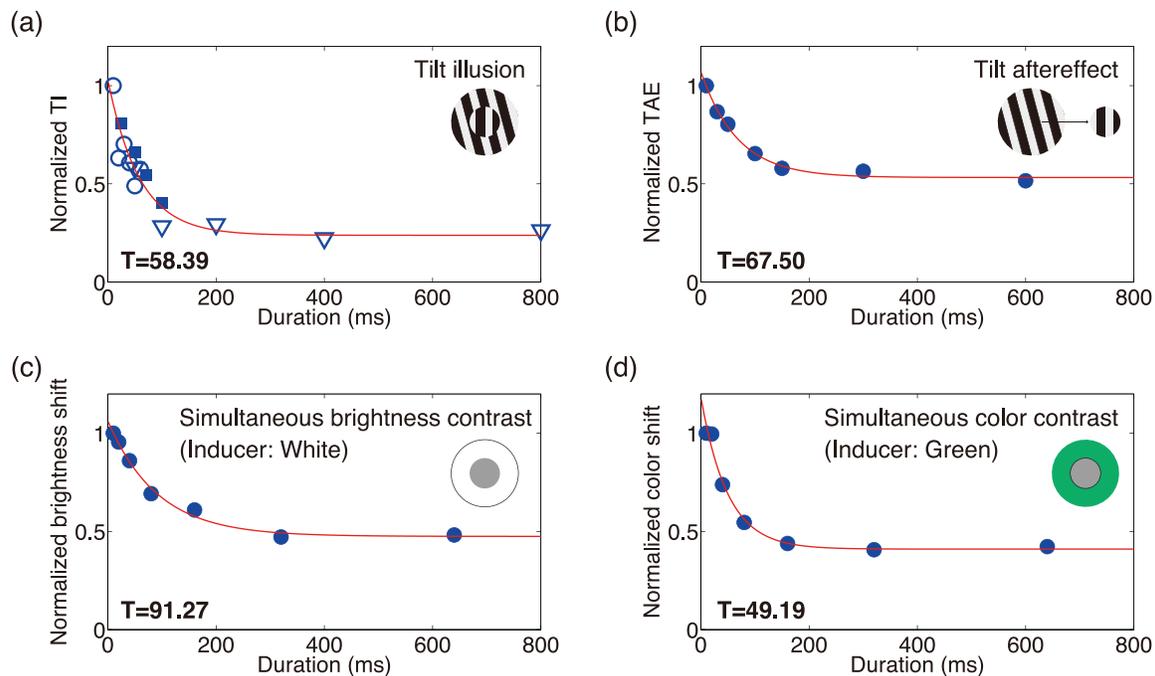
Figure 4. Exponential decay of the illusions with increasing stimulus duration. Plotted data points are (a) tilt illusion data replotted from Wenderoth and Johnstone (1988; squares and triangles, their experiments 1 and 2) and Wenderoth and van der Zwan (1989; circles, their experiment 1), (b) tilt aftereffect data replotted from Wolfe (1984; note that "duration" is of the test, not the adaptation), (c) simultaneous brightness contrast data from Kaneko and Murakami (2012), and (d) simultaneous saturation contrast data from Kaneko and Murakami, both using the mean-luminance gray test patches. Panels a and b were read from figures in respective articles. Panels c and d are mean data from the same three observers who participated in both experiments. Plotted data points are group data and normalized so that the illusion strength at shortest duration is one. Fitted red curves are exponential decay functions, $K \times \exp(-t/T) + C$, where K, T, C are the free parameters. Time constants are shown at the bottom left corner of each panel.

A recent psychophysical study proposed an analogy between color perception and orientation perception (Klauke & Wachtler, 2015). They proposed a multiple-channel color process similar to the model suggested for orientation perception (cf. Gilbert & Wiesel, 1990). Perceived hue is based upon a weighted average of the population response (a population coding model; Klauke & Wachtler, 2015; Wachtler et al., 2003; see also Kuriki, 2007). Klauke and Wachtler (2015) directly compared the human perception data with Wachtler et al.'s (2003) simulation and showed these to be qualitatively similar. In addition, a recent fMRI study (Kuriki et al., 2015) supports the presence of multiple hue-selective mechanisms in human V1 as were found in macaque V1 (Hanazawa et al., 2000; Lennie, Krauskopf, & Sclar, 1990; Wachtler et al., 2003).

Orientation-selective neurons (Ringach et al., 1997, 2003) and hue-selective neurons (Cottaris & De Valois, 1998) in V1 both follow a similar "buildup" process of tuning within several tens of milliseconds; this time, scale is comparable with the temporal property of the enhancement of simultaneous contrast effects observed in Experiments 1 and 2. One may argue that a recent psychophysical study using color naming and discrimination tasks (Cropper et al., 2013) can be counterev-

idence against this similarity: No significant difference was found when stimulus duration was shortened to 50 ms compared with 500 ms. However, the length of 50 ms is not short enough with respect to the dynamics of V1 neurons (Cottaris & De Valois, 1998; Ringach et al., 1999) as well as the time constants derived from psychophysical results (Figure 4; see next section for details). In addition, there are structural similarities between spatially antagonistic suppression for simultaneous contrast mechanisms and suppressive links from neurons selective to nearby directions in hue-selective (Sato, Katsuyama, Tamura, Hata, & Tsumoto, 1994) and orientation-selective (Crook, Kisvárday, & Eysel, 1997; Sato, Katsuyama, Tamura, Hata, & Tsumoto, 1996) mechanisms. Hence, the dynamic property of tuning selectivity (i.e., the "buildup" process) in V1 neurons could be more relevant to simultaneous contrast effects rather than color naming or discriminating characteristics.

To summarize, spatial contextual modulations of V1 neurons and their population responses seem to be likely candidates for the neural basis for simultaneous hue contrast.

Exponential decrease of illusions with increasing duration: Tilt illusion, tilt aftereffect, simultaneous brightness, and saturation contrast

Some previous studies examined the relationship between the illusion strength and the stimulus duration (mostly in the subsecond range). Here we shall mention their interesting similarities across illusions. Figure 4 shows the similarities in the time course of four illusions. For the sake of comparison, all the data were normalized to one at the shortest duration in each study, 10 ms. Wenderoth and Johnstone (1988) and Wenderoth and van der Zwan (1989) examined the tilt illusion strength at different durations, both using 15° inducers. Their data showed very strong tilt illusions at their shortest duration condition (10 ms), decreasing with duration up to 100 ms and remaining the same thereafter (Figure 4a). Striking similarity is seen in Wolfe (1984); he examined the strength of the tilt aftereffect at different test durations. It had been suggested that the tilt illusion and tilt aftereffect involve the same mechanisms (e.g., Magnussen & Kurtenbach, 1980), and indeed Wolfe's graph of the illusion strength versus duration had a temporal profile similar to the tilt illusion graphs (Figure 4b). Intriguingly, Kaneko and Murakami (2012) also measured the effect of stimulus duration on brightness and saturation contrast and found a very similar exponential decrease in strength, commonly found in all the luminance and color inducer conditions. Figure 4c and d show the normalized mean of measured brightness and color shift for three observers who participated in both conditions (Figure 4c and d show only one of four conditions, respectively, for brightness and color condition, but the data are very similar for the rest of the conditions [not shown]).

Time constants were acquired by fitting a simple exponential decay function, $f(t) = K \times \exp(-t/T) + C$, to each set of data points in Figure 4. Red curves in Figure 4 show the fitted results. The obtained time constants were all <100 ms. The strikingly similar time courses of these different visual illusions suggest that they may be based on common principles.

However, not all spatial context effects show the same temporal dynamics. One known example is White's effect (White, 1979). Robinson and de Sa (2008) found inconsistent results for White's effect, which could be seen with short exposure time (83 ms), but did not show any clear increase or decrease at longer exposure times. White's effect is thought to include both contrast and assimilation components (S. M. Anstis, 2005; Clifford & Spehar, 2003). Specifically, when the spatial frequency of the square wave–inducing pattern is 0.5 c/° or less, then the induction effects are entirely due to contrast, not assimilation (Blakeslee, Padmanabhan, & McCourt, 2016). How-

ever, assimilation does play a role for stimuli with high spatial frequency–inducing patterns (Blakeslee & McCourt, 2004). These facts may explain why White's effect differs temporally from simple simultaneous contrast.

The temporal properties of correlated brain activity suggested that V1 is largely responsible for White's effect (McCourt & Foxe, 2004). We have no evidence for negative relationships between stimulus duration and the illusion strength in other kinds of context effects, such as spatial frequency–contrast (Klein et al., 1974), blur–contrast (S. M. Webster et al., 2001), or contrast–contrast effects (Chubb et al., 1989). Further studies are needed on the temporal properties of such illusions.

Possible mechanisms of exponential temporal decrease of simultaneous contrast effects

Assuming that the temporal decreases of simultaneous contrast for orientation, brightness, and color all have a common (or similar) underlying mechanism, what would that be? Experiment 1 showed that the observed increase in the tilt illusion at very short durations was multiplicative, which indicates a shared source for the illusion at all stimulus durations. Therefore, the illusion strength is probably modulated by gain control of such a source mechanism. Extrapolating from these tilt illusion data, we speculate that such gain control also controls hue contrast in Experiment 2.

As we already demonstrated in Figure 4, the illusion strength increases only at very short duration ranges, ~100 ms. This suggests such gain control occurs quickly and stays active within ~100 ms, then is complete after that in our early response to the stimulus. Data from previous physiological studies suggest that it is not unreasonable to assume such time courses. Most of the early visual cells (at retina, LGN, or V1) respond vigorously to the onset of the stimulus regardless of whether they are classically labeled as "transient" or "sustained" (Cleland, Dubin, & Levick, 1971; Enroth-Cugell & Robson, 1966; Ikeda & Wright, 1974, 1975; Müller, Metha, Krauskopf, & Lennie, 2001; Tolhurst, Walker, Thompson, & Dean, 1980). The response decays exponentially, and its time constant is mostly, indeed, tens of milliseconds (Müller et al., 2001), which coincidentally resembles the illusion-duration functions in Figure 4.

In some visual cells, a stimulus outside their receptive fields (RFs) was found to modulate their responses. These spatial contextual effects were maximal within the first 100 ms (Li et al., 2000; see their figure 4-8C; Wachtler et al., 2003; see their figure 4).

These studies show that both the direct response to the stimulus and the spatial contextual effect can appear early (<100 ms) in our visual neural responses, which is consistent with the perceptual responses.

These low-level visual cells have sometimes been regarded as linear filters, implicitly assuming their time-invariant features, but there are recent studies showing their dynamic natures. Specifically, orientation selectivity (Ringach et al., 1997; 2003) and color/hue selectivity (Cottaris & De Valois, 1998) in V1 cells were shown to alter dynamically within the first tens of milliseconds (tuning width change, tuning shift, etc). It was claimed that such dynamic changes were brought about by intracortical interaction involving feed-forward/feedback networks (Ringach et al., 1997). We speculate, from this, that the gain control of the perceptual effect, i.e., the initial decline in the illusion that we observed, may be derived from such interactions including feedback signals. We believe that the decay of the illusion seen at longer durations arises from these ongoing interactions. This process is quick enough to be done and reflected in the percept in the "steady" (500 ms) stimulus but not instantaneous so that it is *not* reflected in the percept in the "flash" stimulus (10 ms).

The idea of interaction with higher-tier processing mediating the gain of the lower-tier processing—in other words, the involvement of multiple stages in the simultaneous contrast effects—is more consistent with the known facts than simple low-level processing. For example, typical V1 RF size is 1°–2° at most (Blakemore & Tobin, 1972; Gilbert & Wiesel, 1990; Li et al., 2000); therefore, multiple RFs should be somehow integrated to represent the whole stimulus; this would be easily done by higher cells with inputs from multiple lower cells. Also, mid- to high-level factors (such as Gestalt grouping, depth perception) that have been shown to affect simultaneous contrast (Economou, Zdravković, & Gilchrist, 2015; Gilchrist, 1977; Horiuchi et al., 2014; but see Blakeslee & McCourt, 2012, for a critical view) are difficult to explain with just low-level processing. Furthermore, it is consistent with a published theoretical model based on perceptual learning studies. This "reverse hierarchy" theory postulates a fast, feed-forward pathway ("vision at a glance") and a slower, recurring feedback pathway ("vision with scrutiny") in our visual information processing (Ahissar & Hochstein, 1997; Hochstein & Ahissar, 2002). Fast pathways correspond to almost automatic or implicit perception, and slow pathways provide a feedback signal going down to lower-level visual processes, add details to the information, and modify the low-level processing accordingly. This theory is consistent with our hypothesis of gain control from higher-level processing.

Conclusions

We demonstrated that brief exposure enhanced simultaneous contrast for tilt illusion and unique yellow hue shift, consistent with Kaneko and Murakami's (2012) findings for brightness and color. The similar temporal dynamics of different visual illusions suggest a common underlying mechanism. Further studies should reveal how universal these dynamic visual strategies are across different visual features.

Keywords: simultaneous contrast, tilt illusion, unique hue

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