

Low-level motion analysis of color and luminance for perception of 2D and 3D motion

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We investigated the low-level motion mechanisms for color and luminance and their integration process using 2D and 3D motion aftereffects (MAEs). The 2D and 3D MAEs obtained in equiluminant color gratings showed that the visual system has the low-level motion mechanism for color motion as well as for luminance motion. The 3D MAE is an MAE for motion in depth after monocular motion adaptation. Apparent 3D motion can be perceived after prolonged exposure of one eye to lateral motion because the difference in motion signal between the adapted and unadapted eyes generates interocular velocity differences (IOVDs). Since IOVDs cannot be analyzed by the high-level motion mechanism of feature tracking, we conclude that a low-level motion mechanism is responsible for the 3D MAE. Since we found different temporal frequency characteristics between the color and luminance stimuli, MAEs in the equiluminant color stimuli cannot be attributed to a residual luminance component in the color stimulus. Although a similar MAE was found with a luminance and a color test both for 2D and 3D motion judgments after adapting to either color or luminance motion, temporal frequency characteristics were different between the color and luminance adaptation. The visual system must have a low-level motion mechanism for color signals as for luminance ones. We also found that color and luminance motion signals are integrated monocularly before IOVD analysis, showing a cross adaptation effect between color and luminance stimuli. This was supported by an experiment with dichoptic presentations of color and luminance tests. In the experiment, color and luminance tests were presented in the different eyes dichoptically with four different combinations of test and adaptation: color or luminance test in the adapted eye after color or luminance adaptation. Findings of little or no influence of the adaptation/test combinations indicate the integration of color and luminance motion signals prior to the binocular IOVD process.

Keywords: motion-in-depth, color, motion aftereffect

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Introduction

After decades of intensive investigations of visual motion perception (Burr & Thompson, 2011; Nishida, 2011), questions remain in the field. One of the most essential questions concerns the visual pathways of motion signals, particularly the relationship of color and luminance motion and their integration process (Cropper, 2005, 2006; Cropper & Wuerger, 2005). That

is, whether color contributes to motion as luminance, and if so, how color and luminance signals are integrated into motion analysis.

Researchers have investigated whether color contributes to motion perception and the answer is apparently “yes.” Although early studies emphasized segregation of motion and color showing weak or no motion sensation in equiluminance color stimuli (Lindsey & Teller, 1990; Livingstone & Hubel, 1988; Ramachandran & Gregory, 1978; Teller & Lindsey,

1993; Webster & Mollon, 1997), later studies confirmed that unambiguous motion perception in color stimuli without luminance signals (Cavanagh et al., 1998; Cropper & Derrington, 1996; Dougherty, Press, & Wandell, 1999; McKeefry & Burton, 2009; Thiele, Rezec, & Dobkins, 2002). Integration of color and motion signals is also supported by contingent aftereffects between them (Favreau, Emerson, & Corballis, 1972; Hepler, 1968).

However, the question of the color motion pathway remains unanswered. A critical aspect in this question is whether color signals are processed in the same manner as luminance signals. The analysis of luminance motion is thought to start as spatiotemporal filtering (low-level motion analysis) (Adelson & Bergen, 1985; Watson & Ahumada, 1985). Whether there is a low-level motion process for color motion has been in debate after confirmation of color contribution to motion perception. Motion perception in equiluminance color stimuli may be analyzed at a higher motion stage than that for spatiotemporal filtering. Indeed, it has been suggested that the perception of motion of color stimuli is related to more complex analysis such as feature tracking with attention (Cavanagh, 1992; Culham & Cavanagh, 1994; Culham, Verstraten, Ashida, & Cavanagh, 2000; Krauskopf & Li, 1999; Lu, Qian, & Liu, 2004; McKeefry, Laviers, & McGraw, 2006; Mullen, Yoshizawa, & Baker, 2003; Seiffert & Cavanagh, 1999; Yoshizawa, Mullen, & Baker, 2000, 2003).

Some studies support low-level motion processing of color signals, while others do not. This is supported by the motion aftereffect of equiluminant color stimuli (Cavanagh & Favreau, 1985; Derrington & Badcock, 1985; Mullen & Baker, 1985), the higher sensitivity of color to motion than that of luminance in terms of cone contrast (Stromeyer, Kronauer, Ryu, Chaparro, & Eskew, 1995) and similar attention effect for chromatic and achromatic motion processing (Dobkins, Rezec, & Kregelberg, 2007). Low-level motion processing of color signals is also supported by the fact that color information does not act like low contrast luminance; i.e., differences in speed discrimination threshold (McKeefry & Burton, 2009) and the addition of color contrast to luminance motion stimuli decreased, instead of increased, the perceived speed (Cavanagh & Favreau, 1985). Low-level motion processing of color signals is questioned by studies that showed possible contributions of the luminance mechanism in color stimuli (Mullen et al., 2003; Yoshizawa et al., 2000, 2003), possible influence of variable equal luminance points of individual cells (Thiele, Dobkins, & Albright, 1999), and the effect of chromatic aberration (Faubert, Bilodeau, & Simonet, 2000).

The discrepancy in the literature could be attributed to the difference in experimental conditions, specifically in stimulus size. In their critical review, Cropper and

Wuerger concluded that low-level color motion process is localized at the fovea (Cropper, 2005, 2006; Cropper & Wuerger, 2005). As their review suggests, the general trend indicates that there is a low-level color motion process. Although it is not easy to isolate it, careful experiments may have succeeded (Cropper, 2005, 2006; McKeefry et al., 2006; Seiffert & Cavanagh, 1999). However, it is crucial to conduct experiments considering the two factors described below, to prove that a low-level color process exists.

To examine whether there is a low-level motion process for color motion, there are two critical factors that must be considered. First, the perception should not be attributed to feature tracking. Second, the perception should not be attributed to residual luminance signals in the color stimulus, either on the retina due to chromatic aberration or in the neural process due to, for example, variable equal luminance points of individual cells (or other unknown factors). No previous study, to our knowledge, realized the condition where there was no possible effect of residual luminance and features that can be tracked.

The MAE is one of the most suitable phenomena for proving the existence of low-level motion signals. The MAE is a negative aftereffect of motion perception seen in a static image after prolonged motion presentation. However, no MAE experiments in previous studies were designed to eliminate the influence of the two factors perfectly. First, it appeared to be impossible to remove any possible effect of luminance artifacts if we consider the variability of equal luminance points for individual cells. Second, apparent motion could be seen by attentive tracking without stimulus motion (Cavanagh, 1992; Shioiri, Cavanagh, Miyamoto, & Yaguchi, 2000; Shioiri, Yamamoto, Kageyama, & Yaguchi, 2002; Verstraten, Cavanagh, & Labianca, 2000) and apparent shift of position changes caused by MAE (Nishida & Johnston, 1999; Snowden, 1998) might be used for feature tracking.

In this study, we report direct evidence of the low-level motion process for color motion signals. We distinguished the low-level motion from feature tracking using MAE of motion in depth, and we distinguished the color mechanism from the luminance mechanism based on differences in temporal frequency characteristics. We also identified the integration stage of color and luminance motion signals required before binocular integration.

The MAE of motion in depth (3D MAE) can be perceived after monocular motion adaptation through the mechanism of analyzing interocular velocity difference (IOVD) (Shioiri, Kakehi, Tashiro, & Yaguchi, 2009). The IOVD is the direction and/or speed difference between the left and right retinal images, which can be caused by motion in depth of objects (Cumming & Parker, 1994; Regan, 1993; Shioiri,

Saisho, & Yaguchi, 2000) and motion in depth perception through IOVD can be explained by a model with detection of monocular motion energy (Shioiri, Matsubara, & Matsumiya, 2012; Shioiri, Nakajima, Kakehi, & Yaguchi, 2008). Prolonged exposure of one eye to lateral motion (monocular motion adaptation) influences motion-in-depth perception (Brooks, 2002; Fernandez & Farell, 2005, 2006; see also Sakano, Allison, & Howard, 2012) and generates 3D MAE (Shioiri et al., 2009). Since MAE is less in the unadapted eye, a static image observed binocularly generates an IOVD. The IOVD signal generates perception of motion in depth.

If 3D MAE is seen with binocularly uncorrelated equiluminance color stimulus, it should be interpreted as the effect of low-level motion. In such a stimulus, temporal and/or spatial binocular rivalry is perceived and only monocular features are seen. Tracking monocular features do not provide any information of motion in depth and there is no feature that can be tracked to see motion in depth in the stimulus. Although MAE may be caused after feature tracking (Culham & Cavanagh, 1994), the MAE is found only with a dynamic test stimulus and is known to be a binocular effect. Feature tracking may cause motion perception when apparent shifts in position are caused by MAE (Nishida & Johnston, 1999; Snowden, 1998), but the motion from tracking shifts in position is a monocular effect; there would be no information for motion in depth.

Temporal properties for color and luminance mechanisms are different in general: bandpass for luminance and lowpass for color. Similar differences have been shown for perception of both motion (Gegenfurtner & Hawken, 1996a) and motion-in-depth (Tyler & Cav-

anagh, 1991). This fact itself does not support the existence of a low-level color motion mechanism. Motion perception in these studies may be based on feature tracking along either 2D or 3D paths. However, there is no feature to track in depth in monocular adaptation. Perception of 3D MAE should be the result of binocular integration of low-level motion signals. Considering these facts, we conclude that there is a low-level color motion mechanism, if a temporally lowpass characteristic is found for 3D MAE with color motion stimuli.

In addition to the isolation of the low-level color motion mechanism, the 3D MAE allows us to investigate the integration stage of color and luminance motion signals. Shioiri et al succeeded in showing that signals from each spatial frequency channel are integrated before they are combined interocularly (Shioiri et al., 2009). They found broad spatial frequency tuning for 3D MAE but spatial frequency selectivity with a narrow band tuning for 2D MAE. Their findings indicate that the IOVD mechanism compares the signals of both eyes after combining motion signals across spatial frequency channels of each eye.

We used the same paradigm as Shioiri et al to investigate the integration of color and luminance motion signals. Color and luminance motion signals may be integrated before or after the IOVD process (Figure 1).

Experiment 1

We measured the duration of 2D and 3D MAEs with different motion speeds or temporal frequencies. After

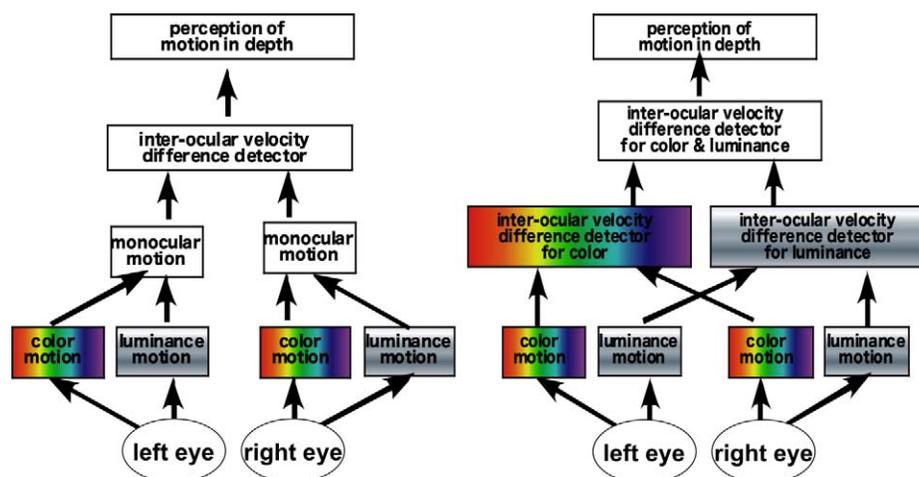


Figure 1. Models for motion in depth through IOVD with color and luminance low-level motion signals. Integration of color and luminance precedes the binocular process for calculating interocular velocity differences (left) and integration of color and luminance follows the binocular process (right). Color-specific and luminance-specific IOVD processes in the left model and a common process for color and luminance in the right model.

monocular adaptation of moving gratings, MAE duration was measured with the same grating but presented binocularly and statically. There are two criteria separately for the 2D and 3D MAEs and they are used in different sessions. The observer pressed a key when MAE of motion in depth disappeared in a 3D MAE session and he pressed a key when lateral MAE disappeared in the identical test stimulus in a 2D MAE session. We used four possible combinations of adaptation and test: color or luminance adaptation with color or luminance test. These conditions are labeled as Ca/Ct, Ca/Lt, La/Lt and La/Ct conditions, where L stands for luminance, C for color, a for adaptation and t for test. Red/green color and achromatic gratings were used.

Method

Stimulus

The experiment consisted of an adaptation phase and a test phase. The adaptation stimuli were a pair of vertical gratings drifting horizontally in opposite directions: always leftward at the top and rightward at the bottom. Spatial frequency was either 0.42 or 1.25 c/deg and the drifting rate was varied between 0.5 and 10 Hz. We used relative motion stimuli since motion in depth is barely perceptible without relative motion components (Erkelens & Collewijn, 1985; Shioiri et al., 2000). Maximum contrast possible in the display was used both for color and luminance: 100% contrast for luminance, the modulation between red and green phosphors for red/green. The CIE 1931 color coordinates were (0.60, 0.33) for red, (0.28, 0.60) for green and (0.44, 0.47) for yellow used for the luminance grating. The yellow used for the luminance condition was the addition of the red and green signals used for the color grating. The areas outside the stimulus regions on the screen were dark (<0.01 cd/m²) throughout the experiment.

The average luminance of the gratings was 30 cd/m² in the luminance and color gratings. For the color gratings, each observer equated luminance of the two colors, minimizing the motion impression. The observer adjusted the luminance of the green against fixed red luminance at 30 cd/m² to achieve the point where impression of motion became weakest. The setting was made with gratings of 1.25 c/deg, moving at 5 Hz presented to both eyes and the equal luminance point (the average of seven settings) was used for all conditions.

The observer viewed the stimuli through a mirror stereoscope to fuse the left and right images. A fixation cross and vertical and horizontal nonius lines were used to aid and confirm the fusion. The test stimulus was a pair of static gratings oriented in opposite directions

($\pm 45^\circ$ from vertical). Opposite orientations of the images were shown to each eye to remove any possible influence of the binocular disparity sensitive mechanism while dichoptic presentation of the images provided an unstable surface with spatially non-uniform binocular rivalry. Even with unstable depth perception, both 2D and 3D MAEs were observed.

Apparatus

Images for each eye were presented on a CRT display (Sony CPD-G500J, Sony, Tokyo, Japan) controlled by a computer (Apple Power Macintosh G4, Apple, Cupertino, CA). The refresh rate was 120 Hz. The observers viewed the display through mirrors arranged to fuse the images at an optical distance of 82 cm. Each stimulus field consisted of 300×300 pixels, which corresponds to a visual angle of $10^\circ \times 10^\circ$. There was a 0.5° central horizontal gap to separate the top and bottom gratings. Note that we used the large stimulus rather than small one for foveal stimulation simply because our first experiment was conducted before Cropper and Wuerger's review (Shioiri, Nakajima, & Yaguchi, 2004).

Procedure

The sequence of a trial was as follows. After checking the alignment of the nonius lines, the observer pressed a key to initiate the presentation of the adaptation stimulus, which lasted for 20 s. The test stimulus was presented 0.5 s after the termination of the adaptation stimulus and lasted until the observer pressed a key to indicate the MAE disappearance. A blank interval was interposed between the trials for 5 s to remove carry-overs of the aftereffect. The uniform yellow field of 30 cd/m² was presented during the interval between the adaptation and the test as well as during the interval between trials. The observers were instructed to indicate the direction of only the depth motion components, ignoring the lateral motion components. This key press also indicated the MAE direction. There were two keys that the observer used to indicate the direction in which the upper half of the stimulus appeared to move. One key indicated approaching motion and the other indicated receding motion. In addition to this 3D MAE criterion, we used a criterion for the disappearance of 2D lateral motion, where the observers were instructed to press a key when the lateral motion disappeared. The 3D MAE direction was indicated in the conditions for 2D MAE criterion to confirm the occurrence of 3D. In general, the 2D MAE disappeared after the 3D MAE. The two criteria were applied in separate sessions.

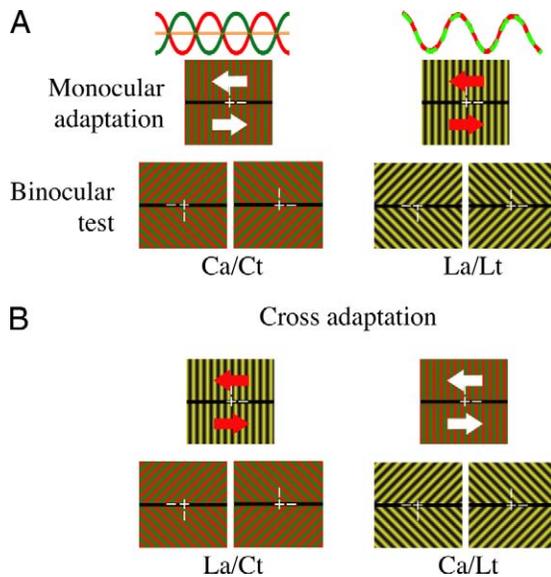


Figure 2. Stimulus conditions for adaptation and test phases. Color and luminance MAE conditions (a) and cross adaptation conditions between them (b).

The adaptation stimulus was presented to either the left or right eye. The stimulus to the other eye was a uniform yellow field with the same luminance as the average luminance of the gratings (30 cd/m^2). The eye for adaptation was chosen randomly from trial to trial while motion direction, spatial and temporal frequencies and test condition were fixed for each session. Two sessions of 10 trials with different motion directions were performed for each spatiotemporal frequency.

The direction of 3D MAE was occasionally ambiguous and the observer's report differed from the prediction of IOVD after monocular MAE. To obtain a stable response, we fixed stimulus conditions in a session except the eye to adapt in Experiments 1 and 2. A percent response to the predicted direction was higher than 95% under all conditions in the experiments. In Experiments 3 and 4, we varied the motion direction and adaptation temporal frequency in a session in addition to the eye to adapt, and we found a lower percentage of the responses to the predicted direction (80.4% on average). Only results with the responses in the predicted direction were analyzed for the MAE duration under all conditions, but including these error trials did not change our conclusions.

The four observers, one author and three naive observers, with normal or corrected-to-normal visual acuity, participated. The experiment started after at least one training session. No feedback to responses was given in either the training or the experimental sessions. All the experiments were conducted in adherence with the tenets of the Declaration of Helsinki.

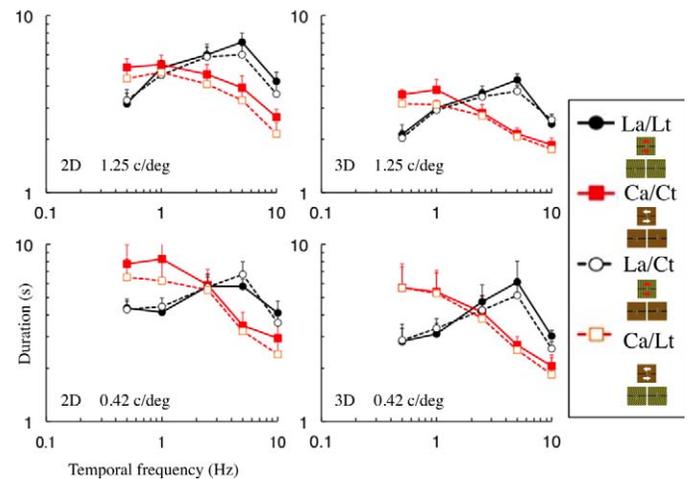


Figure 3. Duration of 2D (left) and 3D (right) MAEs as a function of temporal frequency of motion stimulation in the adaptation phase for 1.25 (top) and 0.42 (bottom) c/deg gratings.

Results and discussion

The results are similar for the two spatial frequencies used (Figure 3). When the adaptation and test stimuli were both luminance gratings (the La/Lt condition), the MAE duration showed a bandpass shape in frequency tuning with a peak around 5 Hz for both 2D and 3D criteria. Results in the Ca/Ct condition, in contrast, showed a lowpass shape in frequency tuning within the range we used (longest MAE at 0.5 Hz). Since any effect of residual luminance should show a temporal frequency tuning similar to that for luminance grating, this lowpass frequency tuning in the Ca/Ct condition indicates that a color mechanism is responsible for both 2D and 3D MAE. It is also important to note that MAE duration is similar for the color and luminance tests. A small effect of residual luminance can hardly explain such a long MAE duration in the Ca/Ct condition, which is similar to that in the La/Lt condition. This leads us to conclude that the visual system must have a low-level motion mechanism for color signals.

A clear cross-adaptation effect was found between the color and luminance stimuli for both 2D and 3D criteria (red symbols in Figure 3). MAE duration was similar in temporal frequency tuning between the Ca/Lt and Ca/Ct conditions although it was slightly longer in the Ca/Ct condition. The MAE duration was also very similar between the La/Lt and La/Ct conditions with slightly longer duration in the La/Lt condition. The results strongly suggest that a common mechanism determined the MAE between the Ca/Lt and Ca/Ct conditions and also between the La/Lt and La/Ct conditions. In addition, the similarity in temporal frequency tuning for color and luminance tests suggests the contribution of a common motion mechanism in

the different tests. This is more than a simple fact of the MAE transfer between the color and luminance stimuli (Cavanagh & Favreau, 1985; Derrington & Badcock, 1985; Mullen & Baker, 1985). The adaptation in the present experiment is suggested to have occurred at or later than the motion mechanism that integrates color and luminance low-level motion signals. That there is only a small effect of selectivity for color and luminance suggests that one motion process that is sensitive to color and luminance may be responsible to the MAE.

Similarity in the cross-adaptation effect between the 2D and 3D MAEs indicates that integration of color and luminance signals precedes binocular integration for IOVD calculation. This revealed that the low-level motion mechanism considered here is a monocular process. One factor we should consider before drawing conclusions from the results is the effect of orientation of test gratings. We used gratings oriented in opposite directions between the two eyes as the test to avoid a possible influence of a disparity detection process. We conducted a control experiment to investigate the effect of orientation difference, using the same test gratings in both eyes. The adaptation temporal frequency was 5 Hz and we compared the MAE with the results at 5 Hz of the original conditions. No significant difference was found between the same and different orientation tests for either the 2D or 3D MAE (Figure 4). The orientation difference between the left and right eye images unlikely influenced MAE duration. We can conclude that there are monocular low-level color and luminance motion mechanisms and that their outputs are integrated also monocularly.

Experiment 2

If a common motion mechanism integrates color and motion monocularly, we expect no difference for any combination of eyes and test stimuli when color and luminance gratings are presented dichoptically. In Experiment 2, we measured MAEs with dichoptic test stimulation, where a luminance stimulus was presented in one eye and a color stimulus was presented in the other. The mechanism that integrates color and luminance motion signals would respond similarly under any combinations of color and luminance stimuli.

Methods

We used the same monocular adaptation as in Experiment 1 but with different test stimuli. The adaptation stimulus were either luminance or color motion presented in one eye. The first test stimulus

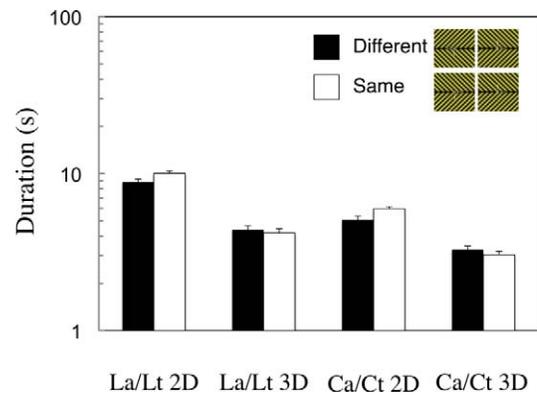


Figure 4. Effect of orientation difference. Dark bars show the results of the test gratings with an orientation difference between the eyes (from the main experiment), and light bars show the results of the same oriented test gratings for both eyes.

consisted of a color test presented in the adapted eye and luminance test in the unadapted eye. The second test stimulus consisted of a luminance test presented in the adapted eye and color test in the unadapted eye. The four combinations of two adaptation and two test conditions were labeled as La/LCt, La/CLt, Ca/CLt and Ca/LCt; the La/CLt condition, for example, denotes the color test in the adapted eye and luminance test in the unadapted eye after luminance adaptation (Figure 5). We also repeated La/Lt and Ca/Ct conditions. One spatial frequency of 1.25 c/deg was used. The same four observers who participated in Experiment 1 took part in this experiment.

Results and discussion

We found little difference among test conditions (Figure 6) after the same adaptation, either luminance motion or color motion. Both MAE durations and temporal frequency tuning are virtually identical for the two test conditions (the LCt and CLt as well as the Lt and Ct) as long as the adaptation stimulus was the same: luminance adaptation resulted in a bandpass shape tuning with a peak at 5Hz and color adaptation resulted in a lowpass shape tuning. These results agree with what is predicted from a monocular motion mechanism that integrates color and luminance motion signals.

Experiment 3

Two opponent color systems, red/green and yellow/blue, have different physiologic origins. Although red/green color stimuli are often used to represent color stimuli, there is no guarantee that the same results

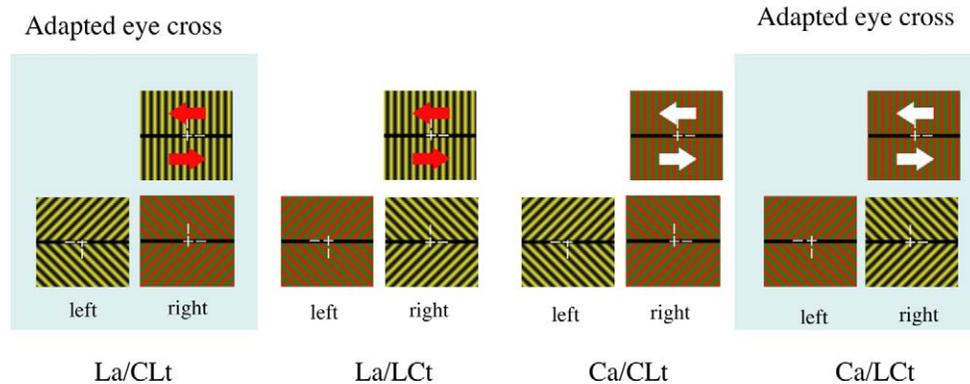


Figure 5. Stimuli for dichoptic test conditions. Color and luminance tests were presented dichoptically under four different conditions. The adaptation stimulus was either color or luminance gratings. The test for the adapted eye was either the color or luminance gratings, which was either the same as or different to the adaptation stimulus. Adaptation stimulus was presented either in left and right eye while the Figure depicts conditions with right eye adaptation.

would be obtained with yellow/blue stimuli. [Experiment 3](#) examined whether the yellow/blue color system contributes to motion perception similarly to the red/green color system.

Methods

We used the same MAE experiment with yellow/blue stimuli in addition to red/green and luminance stimuli. There are several other differences in details from [Experiments 1](#) and [2](#) mostly because we used a different experimental setup from the previous experiments. The drifting rate was varied between 0.5 and 12.5 Hz. The CIE 1931 color coordinates were (0.62, 0.34) for red, (0.29, 0.60) for green, (0.41, 0.51) for yellow and (0.15, 0.07) for blue and the average luminance of the gratings was 14 cd/m². The luminance grating had CIE color coordinates of (0.28, 0.30), which was arbitrarily chosen. One spatial frequency of 1.25 c/deg was used. The stimulus to the unadapted eye was a uniform gray field with 14 cd/m². All temporal frequencies were mixed in a session and three sessions were performed, resulting in 12 trials in each condition (one session consisted of four trials of two adapted eyes multiplied by two motion directions for each condition).

We used heterochromatic flicker photometry to obtain equal luminance point for each observer in [Experiment 3](#), instead of minimum motion impression. This was to confirm that there was no influence of methods to equate luminance conditions. The observer adjusted the green luminance against red luminance of 14 cd/m² in the red/green grating and the yellow luminance against the blue luminance of 14 cd/m² in the yellow/blue grating. The flicker frequency was 15 Hz and 20 settings were made for each condition.

Stimuli for each eye were presented on a CRT display (Sony CPD-G520) controlled by a display card

(Cambridge Research, VSG2/5, Cambridge Research Systems, Rochester, UK) with the refresh rate of 120 Hz. The optical viewing distance was 37 cm and the stimulus field was 140 × 154 pixels or 10° × 11° with a gap of 1° to separate the top and bottom gratings. Four observers, one author and three naive observers, with normal or corrected-to-normal visual acuity participated.

Results

A clear cross-adaptation effect was found between either adaptation-test pairs of the six combinations of the red/green, the yellow/blue and luminance stimuli

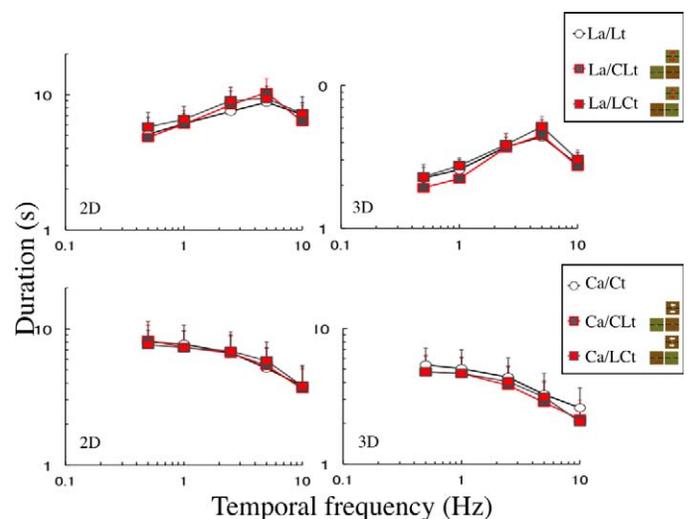


Figure 6. Duration of 2D (left) and 3D (right) MAEs as a function of temporal frequency of motion stimulation in the adaptation phase for luminance (top) and color (bottom) adaptation. Data are averages of the four observers and error bars represent standard error across observers.

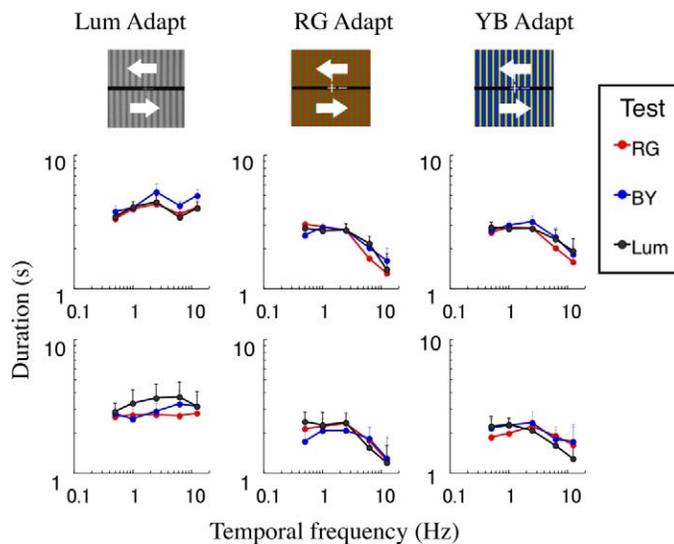


Figure 7. Straight and cross adaptations among luminance, red/green and yellow/blue stimuli. Duration of 2D (top) and 3D (bottom) MAEs are shown as a function of adaptation temporal frequency for luminance (left), red/green (middle) and yellow/blue (right) adaptation conditions. Different symbols represent different test stimuli: black for luminance, red for red/green and blue for yellow/blue. Data are averages of the four observers and error bars represent standard error across observers.

(Figure 7). After luminance adaptation, MAE duration resulted in a bandpass shape tuning for all three color-pair tests for both for 2D and 3D MAEs. After either type of color adaptation, MAE duration resulted in a lowpass shape tuning for all three tests. These results indicate that motion signals of luminance and two color opponent systems are integrated monocularly, and that motion signals of the left and right eyes are subsequently analyzed to generate motion in depth signals through the IOVD.

Experiment 4

We addressed two additional issues in Experiment 4. First, the luminance property estimated with MAE duration may not be the same under low stimulus contrast conditions. We should consider low luminance contrast conditions because the contrast of residual luminance components in equiluminance color stimuli should be low. We measured the MAE with a contrast luminance of 5% in Experiment 4. Second, the color stimuli were not designed to isolate L-M and S mechanisms in Experiment 3 while they were perceptually close to unique red, green, blue and yellow. When low-level mechanisms are considered, we should target the L-M and S, post-receptoral mechanisms. In Experiment 4, we measured the MAE with the color

stimuli modulated along L-M axis and that along S axis in MacLeod-Boynton diagram (Derrington, Krauskopf, & Lennie, 1984; MacLeod & Boynton, 1979; Shioiri & Cavanagh, 2000) based on Smith and Pokorny cone fundamentals (Smith & Pokorny, 1975).

Methods

We used five conditions: straight and cross adaptation/test combinations for two-color stimuli and the low luminance contrast condition. Only the 2D criterion was used because the questions asked here were at the level of monocular processes. The contrast of the luminance stimuli was set to 5%, which was above the threshold at all temporal frequencies used while the visibility was noticeably low at the highest frequency used. CIE 1931 color coordinates of the color pair for the L-M stimulus were (0.351, 0.281) and (0.219, 0.337) and those for the S stimulus were (0.255, 0.215) and (0.379, 0.532). The cone contrast of the color modulation for L-M stimulus was 7.1% and that for S stimulus was 86%. To set the equiluminant, heterochromatic flicker photometry was used. In flickering gratings at 15 Hz, each observer adjusted the luminance of the +L or +S stimulus against the +M or -S stimulus, whose photometric luminance was 67 cd/m². Three participants from Experiment 3 took part. Other experimental details were the same as those in Experiment 3.

Results and discussion

MAE duration with the low luminance contrast stimulus resulted in a bandpass shape tuning as with high contrast stimuli (Figure 8a vs. Figure 7, top left). This confirmed that temporal frequency characteristics are different between color and luminance MAEs for a large range of luminance contrast. There are also differences between the high and low contrast stimuli. First, MAE duration was shorter with the low contrast stimulus. This is not surprising under the assumption that weaker contrast stimuli are less effective to motion mechanisms. Second, the reduction of duration tended to be larger at higher temporal frequencies, showing larger effect of temporal frequency in the present experiment. This may be related to contrast constancy (Georgeson & Sullivan, 1975), which is the invariant perception of apparent contrast with spatial frequency with contrasts of sufficiently above the threshold. To achieve equivalent apparent contrast, less difference in physical contrast is required among different spatial frequencies even the contrast threshold varies dependently on spatial frequencies. Similarly, there may be less effect of adaptation temporal frequency with higher

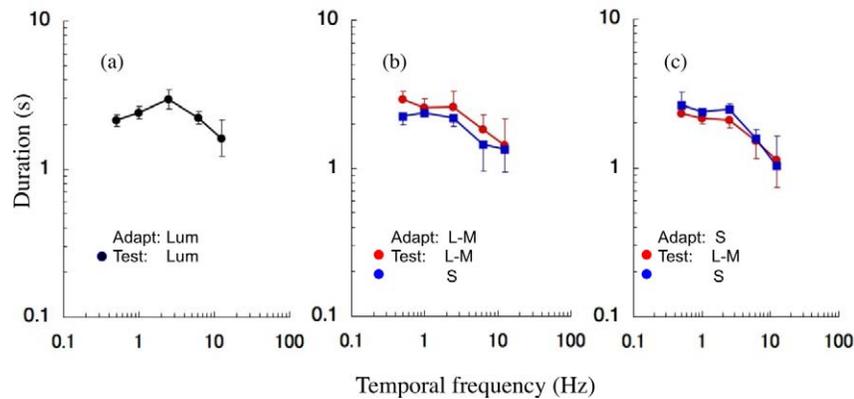


Figure 8. (a) MAE duration for low luminance contrast stimuli. (b) L-M adaptation conditions. (c) S adaptation conditions. Different symbols represent different test stimuli in (b) and (c): red for L-M test and green for S test. Data are averages of the three observers and error bars represent standard error across observers.

stimulus contrast for MAE duration, as less effect of spatial frequency with higher stimulus contrast for a speed threshold measurement (see figure 7 of Yang and Stevenson, 1997).

The results with color stimuli are also similar to previous experiments. MAE duration resulted in a lowpass shape tuning. Little difference is seen among different adaptation/test combinations (Figure 8b, c). These results confirm that the two opponent color systems share a common motion process.

General discussion

We revealed, so far, that there is a low-level color motion mechanism by consideration of two critical factors: the effect of feature tracking and the effect of residual luminance in color stimuli. We used MAE of motion in depth after monocular motion adaptation (3D MAE) to remove the influence of the two factors. First, there is no need to consider the possible influence of the tracking mechanism because motion in depth through IOVD requires different motion information from each eye. The 3D MAE found in the present experiment should reflect the outputs of a low-level motion mechanism, which is at a stage before binocular integration. Second, the difference in temporal frequency tuning for MAE duration between the color and luminance motions ruled out any effect of residual luminance in color stimulus. In all experiments, we found a different temporal frequency tuning between color and luminance adaptations. There should be separate pathways for color and luminance low-level motion signals.

Interestingly, the present results provided little hint of difference in contribution to motion between color and luminance signals. This contrasts with the difference in perceived speed between color and luminance stimuli. Color motion appears to move slower than luminance motion in general (Cavanagh, Tyler, &

Favreau, 1984; Ramachandran & Gregory, 1978). Although contrast is a factor that changes speed perception, perceived speed does not seem to influence MAE durations. During the adaptation in the present experiments, color motion appeared to be slower than luminance motion, but similar MAE durations were found with color and luminance motion adaptation. Perceived speed may not be an appropriate index of motion strength. Our results of longer MAE duration with color than with luminance stimuli at low temporal frequencies suggest that color motion stimuli generate slow but not necessarily weak motion perception.

The difference in temporal tuning indicates that both color and luminance signals are processed through low-level motion mechanisms. In a simple view of two pathways in the early vision, the magnocellular pathway conveys motion signals and the parvocellular pathway conveys color signals (Livingstone & Hubel, 1988). In this view, there is no place for the low-level motion mechanism for color signals. However, this view is too simple and not supported by recent studies. First, the parvo-pathway may be sensitive to the slow motion of color and luminance. Although temporal sensitivity tuning of the parvo-pathway is lowpass and the pathway is less sensitive to fast motion, several studies have suggested that there is a mechanism sensitive to slow motion in addition to one sensitive to fast motion (Alais, Verstraten, & Burr, 2005; Gegenfurtner & Hawken, 1996b; Hawken & Gegenfurtner, 2001; Hawken, Gegenfurtner, & Tang, 1994; Shioiri & Matsumiya, 2009; van der Smagt, Verstraten, & van de Grind, 1999; Verstraten, van der Smagt, & van de Grind, 1998). Sensitivity to low temporal frequencies is suited to convey slow motion signals. Sensitivity to motion in V4 cells has been reported, and the parvo-pathway may convey motion signals (Cheng, Hasegawa, Saleem, & Tanaka, 1994; Desimone & Schein, 1987; Ferrera & Maunsell, 2005; Ferrera, Rudolph, & Maunsell, 1994; Gegenfurtner & Hawken,

1996a; Mountcastle, Motter, Steinmetz, & Sestokas, 1987; Tolia, Keliris, Smirnakis, & Logothetis, 2005). Second, contribution of color signals to luminance or the magno-pathway has also been shown at an early stage in the visual (Smith, Lee, Pokorny, Martin, & Valberg, 1992; Tsujimura, Shioiri, Hirai, & Yaguchi, 1999; Tsujimura, Shioiri, & Nuruki, 2007). Recent studies have revealed sensitivities of MT to color motion. There are MT cells that respond to stimuli modulated along L-M or S-cone directions (Barberini, Cohen, Wandell, & Newsome, 2005; Liu & Wandell, 2005; Mullen, Thompson, & Hess, 2010; Thiele et al., 1999; Thiele, Dobkins, & Albright, 2001; Thiele et al., 2002; Wandell et al., 1999). Note that weak sensitivity to S-cone direction to MT shown in these studies is consistent with our finding of similar MAE between L-M and S stimuli with much higher cone contrast of S stimulus (86% for S stimulus and 7.1% for L-M stimulus).

Although color motion effect in the previous studies may or may not be pure low-level color motion effect, our finding of contribution of the opponent color systems is perhaps related to the color motion in the parvo-pathway (and konio-pathway for S stimulus) or to the contribution of color signals to the magno-pathway, while we cannot decide which is a more appropriate assumption here.

It is of interest to consider our results and those of Mullen and colleagues (Mullen et al., 2003; Yoshizawa et al., 2000, 2003) in terms of a common mechanism for color and luminance motion signals. A typical receptive field model with a retinal cone mosaic that assumes inhibitory input from surround with temporal delay predicts sensitivity to color motion signals at low temporal and low spatial frequency stimulations and sensitivity to luminance motion at high temporal and low spatial frequency stimulations (Ingling & Martinez-Uriegas, 1985). Physiologic studies also showed the sensitivity to color at low temporal frequencies. The results of the cross masking effect between color and luminance reported by Mullen and colleagues (Mullen et al., 2003; Yoshizawa et al., 2000, 2003) indicate that there is a mechanism sensitive to color motion interacts with luminance motion, while they did not consider the mechanism as low-level color motion mechanism. Our finding of differences in temporal characteristics and similarity between MAE of the color and luminance stimuli indicate that there is a motion process for color signals that cannot simply be attributed to luminance artifacts. If we assume a motion mechanism that is sensitive to both color and luminance, the mechanism could explain both our results and those of Mullen and colleagues. Both the masking effect and cross adaptation should occur at the site of the mechanism. Although this is no more than a speculation, this is one of the simplest interpretations of the present

results. In this interpretation, we may need another color motion mechanism to explain color motion perception that is not influenced by luminance signals and limited to fovea (Cropper, 2005, 2006). Since our stimulus size of 10° was large and the results suggest that color and luminance motion signals are processed together, the underlying mechanism is not likely to be the same as the pure color motion detector identified by Cropper. We could also relate the possible difference across visual field to the finding of different interaction between color and luminance in an MAE experiment (McKeefry et al., 2006). McKeefry reported that MAE exhibited a high degree of chromatic selectivity while position shift caused by MAE showed cross adaptation effect between color and luminance. Although this supports the different analyses between motion and position processes, it might be possible that the difference is attributed to the different retinal locations of stimulus between the two tasks: the motion stimulus was presented in the fovea while the pair of position stimuli was presented 1.9° above and below the fovea. Foveal stimulation may be critical to show selectivity in luminance and color signals.

The monocular integration of color and luminance is also an important finding of the present experiments. This supports the presumption that the low-level motion mechanism for color is at a monocular site. Therefore, MT is not necessarily a candidate for the site of color motion processing since MT cells are known to be binocular (Maunsell & van Essen, 1983; Zeki, 1974). Although MT is regarded to be the center for motion analysis, a considerable percentage of cells in other areas, such as V3d, V3a, V3v and V4, have sensitivity to motion (Dupont, Orban, De Bruyn, Verbruggen, & Mortelmans, 1994; Felleman & Van Essen, 1987; Gegenfurtner, Kiper, & Levitt, 1997; McKeefry, Burton, & Morland, 2010; Smith, Greenlee, Singh, Kraemer, & Hennig, 1998; Tootell et al., 1995; Wandell, Dumoulin, & Brewer, 2007). If MT is a site for motion in depth through IOVD as suggested by an fMRI study (Rokers, Cormack, & Huk, 2009), it may be the case that MT cells read motion signals from a monocular motion stage to calculate the IOVD.

The present study provided evidence of color motion processing at an early stage of visual processing. We conclude that the analysis of color motion is essentially the same as that of luminance, and that the difference between the color and luminance motion analyses is the difference in speed tuning.

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