

Human Visual System Integrates Color Signals along a Motion Trajectory

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Summary

Whether fundamental visual attributes, such as color, motion, and shape, are analyzed separately in specialized pathways has been one of the central questions of visual neuroscience [1–3]. Although recent studies have revealed various forms of cross-attribute interactions, including significant contributions of color signals to motion processing [4–9], it is still widely believed that color perception is relatively independent of motion processing. Here, we report a new color illusion, motion-induced color mixing, in which moving bars, the color of each of which alternates between two colors (e.g., red and green), are perceived as the mixed color (e.g., yellow) even though the two colors are never superimposed on the retina. The magnitude of color mixture is significantly stronger than that expected from direction-insensitive spatial integration of color signals [10, 11]. This illusion cannot be ascribed to optical image blurs, including those induced by chromatic aberration [12, 13], or to involuntary eye movements of the observer. Our findings indicate that color signals are integrated not only at the same retinal location, but also along a motion trajectory. It is possible that this neural mechanism helps us to see veridical colors for moving objects by reducing motion blur, as in the case of luminance-based pattern perception [14–19].

Results

In our stimulus display (Figures 1A and 1B), moving bars separated by constant intervals jump in one direction

with their color alternating between red and green at every jump. The movement of the bright bars on the dark background results from luminance-based motion. Because the jump size is equal to the bar width, the two different colors are not superimposed on the retina when the eyes are stationary. Nevertheless, the moving bars appear to have a yellowish hue. The comparison is a stimulus in which the bars are flashed simultaneously (Figures 1C and 1D). Given that, at each retinal location, the two stimuli result in spatiotemporal patterns that are similar except for a time displacement, they should generate a similar percept if each bar flash simply remains present for a short time on the retinal coordinates [20, 21] and is spatially integrated by optical mechanisms or by the standard retinotopic (spatiotemporally separable) neural color summation [10, 11]. However, under certain stimulus conditions, whereas the flashed stimulus is seen as red-green stripes, the moving bars appear to have a more yellowish hue.

We verified this observation in a rating experiment. We asked observers to evaluate the magnitude of subjective color mixing by means of a five-point rating scale (with physical samples of various chromatic contrasts used as references) for the motion and flash stimuli while systematically changing the bar width. The stimulus onset asynchrony (SOA) was fixed at a short value (6.25 ms). To check the reliability of the rating, we showed the stimulus with three magnitudes of color mixture—red/green, orange/yellow-green, and yellow/yellow—each corresponding to the reference sample colors for rating 1 (perfect segregation, equivalent to 100% chromatic contrast), 3 (moderate mixture, 50%), and 5 (perfect mixture, 0%). Because these colors were shown in random order, the observers could not tell whether a given stimulus that appeared yellow to them was indeed yellow or a mixture of red and green. The results (Figure 2) show that as the bar width was increased, the mixture rating for the color-alternating motion pattern decreased from the perfectly mixed down to the level set by the true degree of mixture (1, 3, or 5, indicated by an orange dotted line in each panel), irrespective of the type of stimulus. This indicates that the observers' ratings were accurate (they used the scale as instructed) and consistent (they used the same scale for the different stimulus conditions). The reduction of the mixture rating with increasing bar width for the flash stimulus can be ascribed to the retinal-spatial summation of color signals. The critical finding is that for a wide range of bar widths, the mixture rating was higher for the motion pattern than for the flash pattern for all observers we tested (for individual data, see Figure S1 in the Supplemental Data available online).

Motion-induced color mixing was robust to stimulus changes that would be expected to affect the magnitude of color integration. First, a retinal-eccentricity increase, which is expected to enlarge the area of integration [22], enhanced color mixture for both motion and flash stimuli, while keeping their difference nearly the same

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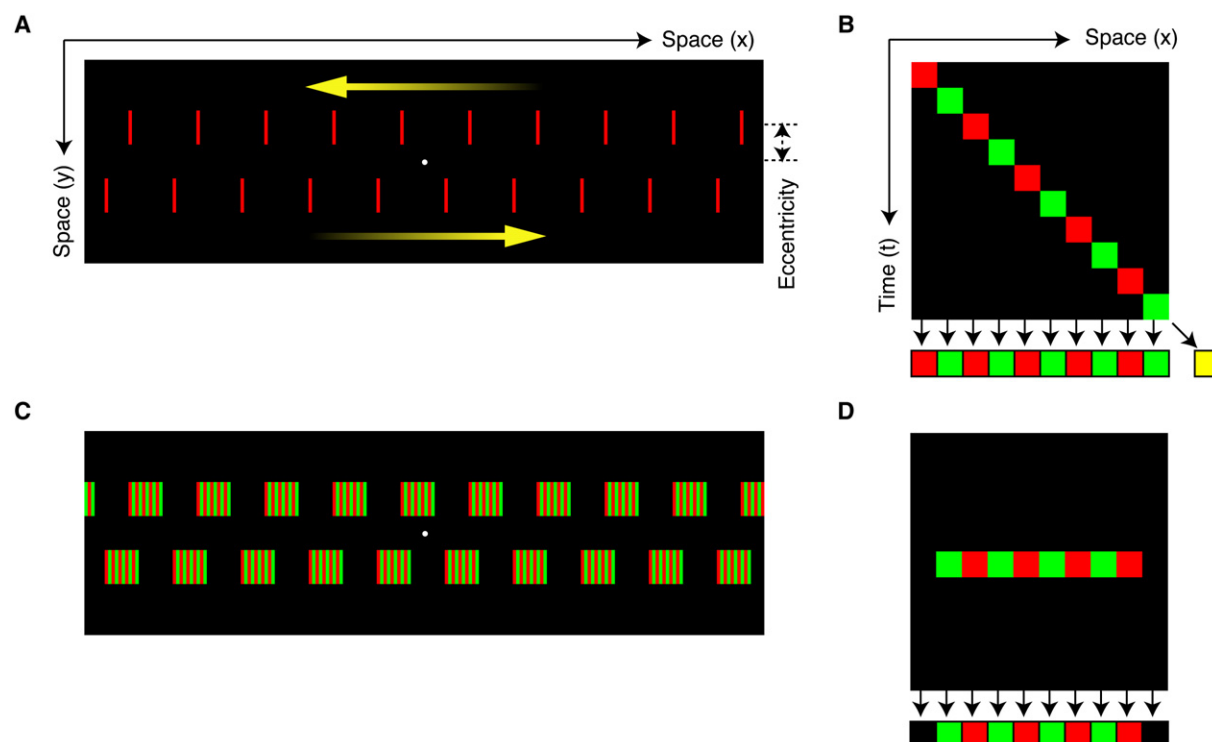


Figure 1. Stimuli Used to Test Motion-Induced Color Mixing

(A) Spatial configuration of a frame of the color-alternating motion stimulus.

(B) Motion trajectory of a bar in the motion stimulus shown in the form of a space-time plot. The bar jumps in one direction with its color alternating between red and green at every jump. The colors integrated over time at each retinal position are shown at the bottom, and the color integrated along the motion trajectory is shown at the bottom right.

(C) Spatial configuration of the control flash stimulus.

(D) Space-time plot of the flash stimulus. Under certain conditions, the moving stimulus is seen as yellowish bars, whereas the flashed stimulus appears as red-green stripes. This difference, which cannot be explained by the classical notion of color integration at each retinal location, demonstrates a new notion of color mixing along a motion trajectory. Demonstrations are available on a public database, Visiome Platform (<http://platform.visiome.neuroinf.jp>).

(compare Figures 2A and 2B). Second, we used two luminance conditions—red and green phosphors were either driven at maximum intensities of the monitor (Figure 2B) or were made subjectively equiluminant (Figure 2C). Although the mixture rating for the former condition was slightly lower, presumably because of the involvement of luminance-sensitive mechanisms with finer spatial resolutions, motion-induced color mixing was similar for both luminance conditions. Third, the effect is not dependent on color axis. Whereas the R-G color axis we used was close to (though did not exactly match) the L-M axis in the standard cone-contrast color space [23, 24], a similar mixing effect was observed for the S axis stimuli (Figure 2D). This result is in marked contrast to the finding that detection of luminance motion is masked by chromatic flicker along the L-M axis but not along the S axis [7]. Finally, motion-induced color mixing was observed even when we did not show premasks and postmasks (Figure S2).

To minimize the tracking of eye movements, we had observers fixate the center of the display and simultaneously judge the colors of two arrays of bars that moved in opposite directions for a very brief period of time (typically 200 ms). Subjectively, color appearance was similar for the two arrays and stable over the period of stimulus presentation. The additional data shown in

Eye-Movement Artifacts in the Supplemental Data (including eye-movement measurements and a double-rating experiment for simultaneously presented motion and stationary stimuli) further excluded the eye-movement artifacts. In addition, a series of experiments reported in **Optical-Blur Artifacts in the Supplemental Data** excluded alternative concerns that motion-induced color mixing might reflect retinal-image degradation caused by physical blur on the display or by optical blur due to accommodation error or chromatic aberrations [12, 13].

When we increased the bar width, we also increased the motion displacement at each jump, which degrades the quality of motion signals [25]. Furthermore, given that the minimum temporal interval to see good apparent motion increases as the spatial displacement increases [26, 27], our use of a short SOA (6.5 ms) may have enhanced deterioration of motion perception for wider bars. This may account for why clear motion-induced color mixing was observed only for narrow bars in Figure 2. To test this possibility, we measured the effect of motion on color mixing while varying both bar width and SOA. The result (Figure 3) shows a clear interaction of the two variables. As the SOA was increased, the magnitude of color mixing decreased for narrow bars, as is expected from the increase of temporal

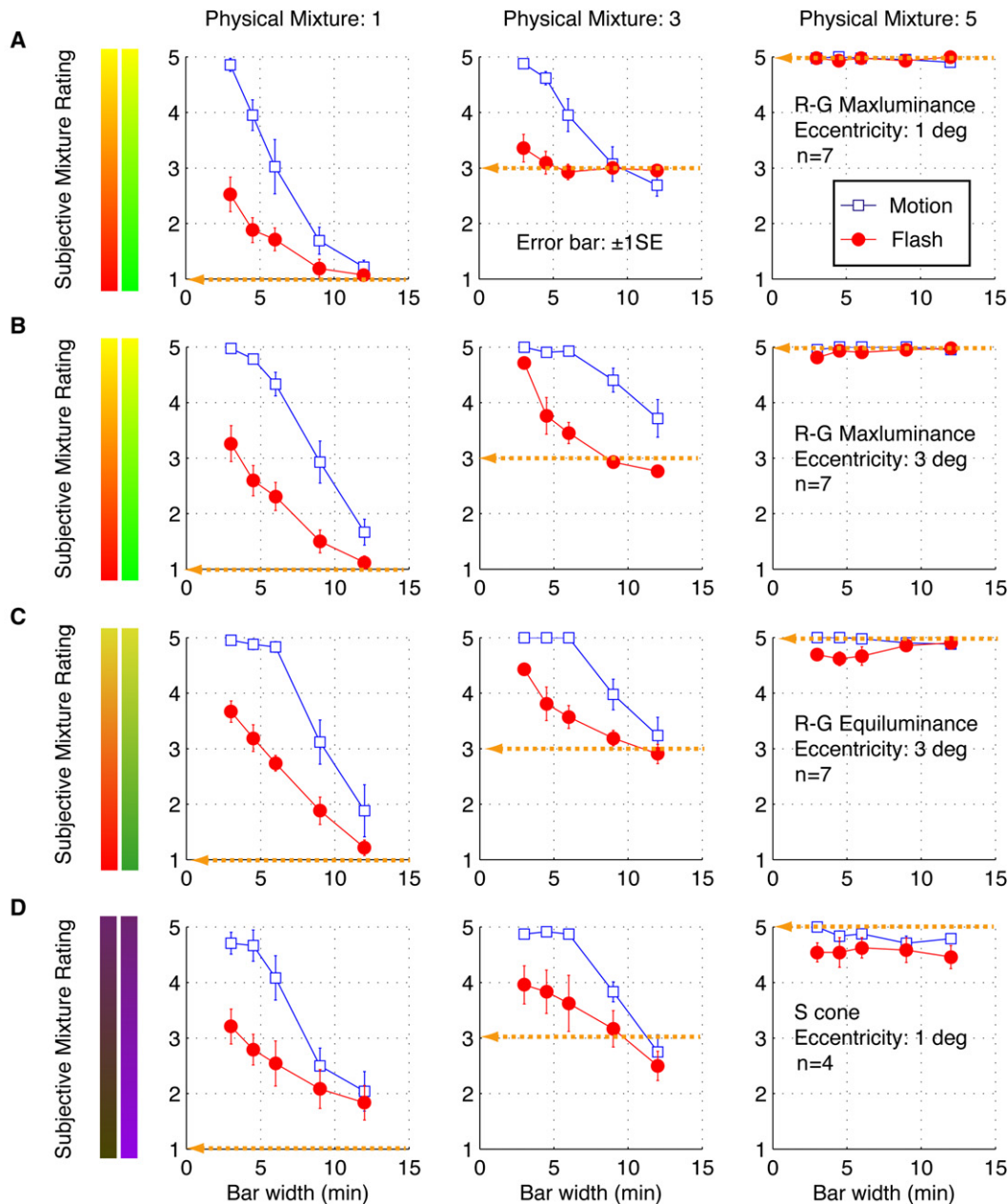


Figure 2. Results of a Rating Experiment for Motion-Induced Color Mixing

(A–D) Rating of color mixture (1–5: perfect segregation–perfect mixture, respectively) is plotted as a function of the width of color bars for the motion and flash stimuli. (A) shows the red-green maxluminance condition (red: 28 cd/m², green: 84 cd/m², 1.0° eccentricity). (B) shows the red-green maxluminance condition, 3.0° eccentricity. (C) shows the red-green equiluminance condition, 3.0° eccentricity. (D) shows the S cone modulation condition, 3.0° eccentricity. In each row, three panels show the ratings for different magnitudes of the physical color mixture of the presented stimulus, indicated by dotted arrows. The pattern of convergence of the rating to the arrowed lines ensures the reliability of the observers' judgments. Error bars indicate the standard error across observers. Each point shows the average for seven (A–C) or four (D) observers (six judgments for each). See also [Supplemental Data of Rating Experiments](#) for additional data. The results indicate that apparent color mixing is stronger for the motion stimulus than for the control flash stimulus.

separation of two colors, whereas the mixture magnitude increased for wider bars. For the longest SOA we used (75 ms), a weak effect of motion remained to be observed even at the widest bars we used (48 min). This interaction was evident when the physical color mixture was moderate (3) more than when it was minimum (1). These results not only suggest that motion signals could affect apparent color mixing in a wide range of spatial scales, but also demonstrate that the strength of

perceived motion is a determinant of the magnitude of color mixing in this phenomenon.

In addition to a rating method, we also evaluated the effect of motion on color mixture in terms of a more objective performance measure (Figure 4). We presented a red/green-alternating motion (or a control flash stimulus) of a given chromatic contrast (target), together with a nontarget stimulus that was identical to the target except that the chromatic contrast was 0%. The observers

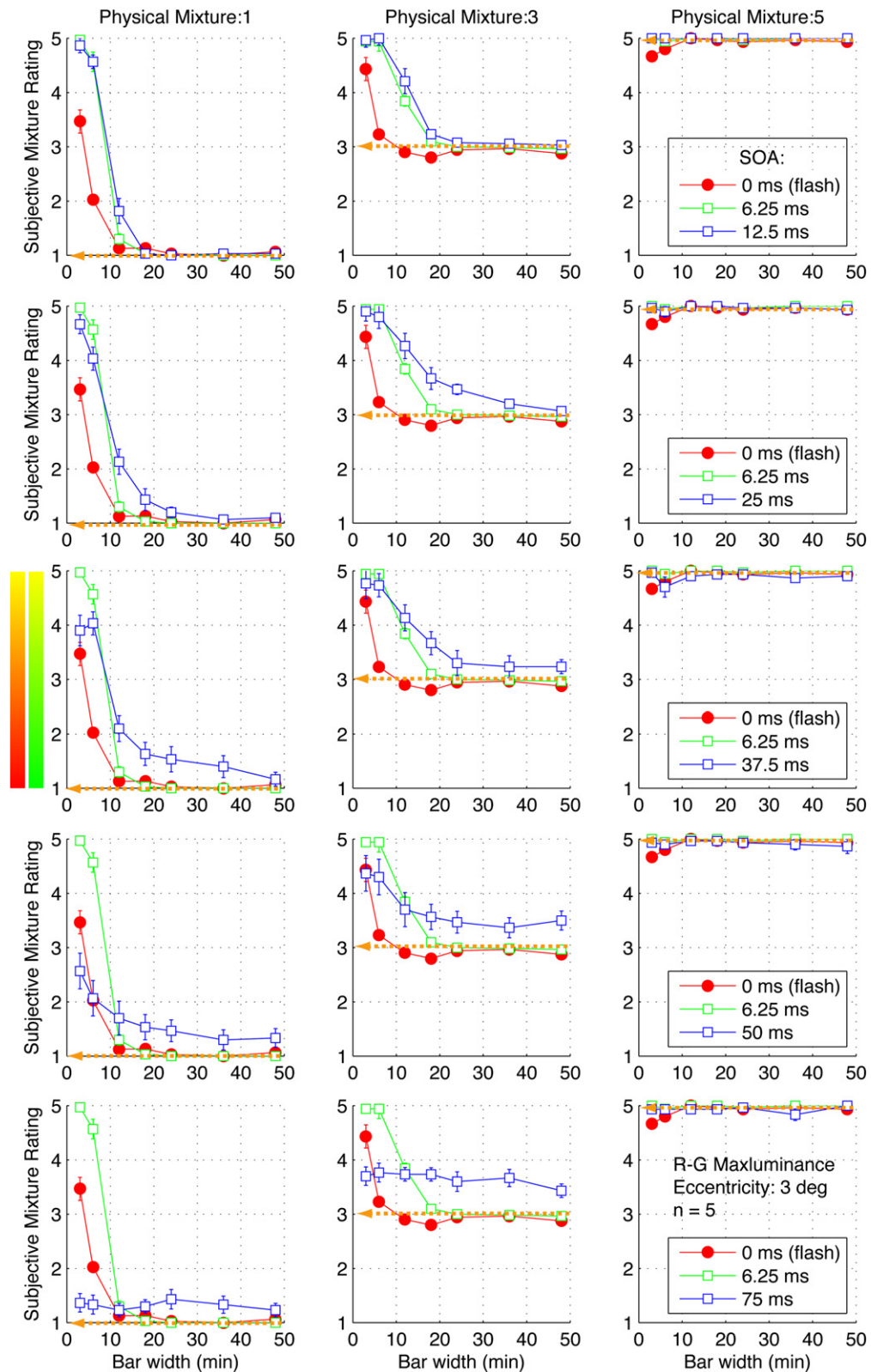


Figure 3. Spatiotemporal Interaction of Motion-Induced Color Mixing

Results of a rating experiment in which stimulus onset asynchrony (SOA) of motion stimuli was varied from 12.5 ms (top panel) to 75 ms (bottom panel). For comparison, the results for control flash stimuli and for motion stimuli with the default shortest SOA (6.25 ms) are shown in all panels. Each point shows the average for five observers. As the SOA was increased, the color mixture rating was reduced for narrow bars and increased for wider bars. Error bars indicate the standard error across observers.

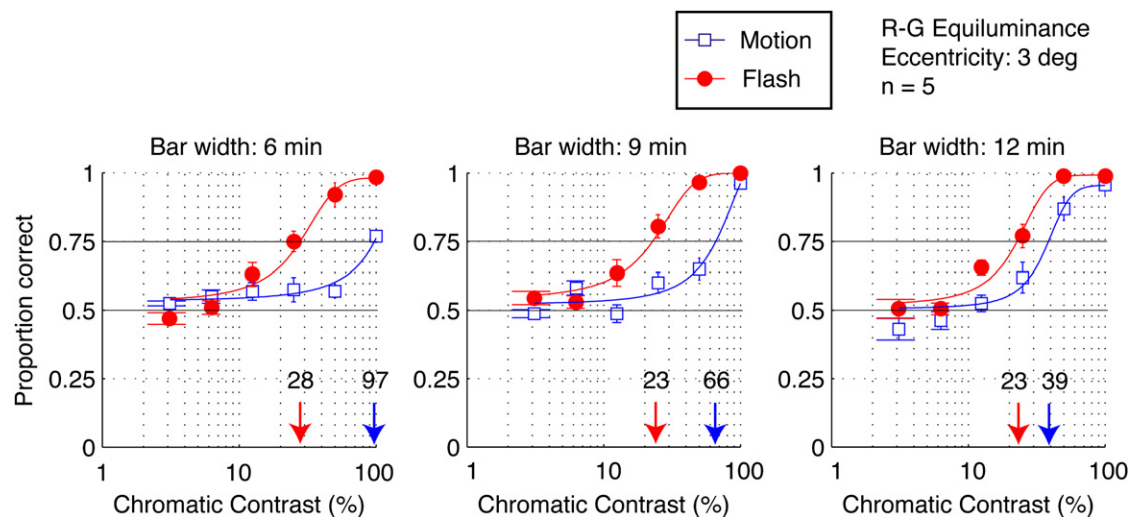


Figure 4. Motion-Induced Color Mixing Indicated by Differences in the Threshold of Discriminating Stimuli with and without Chromatic Contrast
The stimulus was a color-alternating motion (filled red circle) or a control flash stimulus (open blue square). Proportion correct of chromatic-contrast detection as a function of the target chromatic contrast. Each data point shows the average for five observers (40 judgments for each). The smooth curves are best-fit logistic functions, and the arrows indicate the 75% correct points. Error bars indicate the standard error across observers.

had to make a two-alternative forced-choice judgment about which stimulus was the target. We expected that the stronger the magnitude of perceptual color mixing was, the higher would become the contrast required for correct judgment. Indeed, when the bar width was 6 min (the rating data for this bar width indicated a large motion-induced color mixing), the threshold contrast obtained under the motion condition (97%) was more than three times as high as the threshold contrast obtained under the flash condition. As the bar width was increased, the threshold contrast of the motion condition gradually decreased. This mainly reflected a reduction of motion-induced color mixing, rather than a reduction of conventional spatial color mixing, because the threshold contrast of the flash condition remained nearly the same. These results agree well with the findings of the rating method. They further indicate that stimulus motion can change color-detection performance in addition to subjective color appearance, and they objectively prove that motion-induced color mixing is perceptually indistinguishable from physical color mixing.

Discussion

Motion-induced color mixing suggests that the human visual system integrates color signals not only at the same location, but also along the motion trajectory. As compared to the effects of color on motion perception, little attention has been paid to the effects of motion on color perception. The classical Benham's top (subjective color seen in a rotating achromatic pattern) is irrelevant to motion processing [28]. Misbinding of color and motion [29, 30] likely reflects late interactions occurring after completion of basic analysis of color and motion. There is controversy as to what sort of interaction the motion-contingent color aftereffect [31] reflects. A small number of previous studies have addressed direct modulations of color appearance by motion signals. Cicerone et al. [32] reported motion-induced color

spreading, which suggests the summation of color information within a surface defined by common motion [33]. This illusion, along with a couple of demonstrations of motion-induced segmentation of physically mixed colors [34, 35], indicates that when motion affects a spatial representation, it also modulates color perception. In comparison, the present findings reveal a more direct motion-color linkage that cannot be deduced from the previous findings. Recently, Monnier and Shevell [11] examined an effect of stimulus motion on chromatic-pulse detection. Although they reported a finding that might be related to motion-based color integration (i.e., higher detection thresholds for coherent motion than for random motion), the authors only suggested an alternative interpretation in terms of motion-independent spatiotemporal integration.

The visual system integrates sensory signals over time. This could improve the signal-to-noise ratio of input signals. However, when the image moves on the retina, temporal integration at the same retinal location should lead to image degradation. It is known for luminance-defined patterns that the visual system suppresses this motion blur [15]. A proposed mechanism for this motion deblurring (and for spatiotemporal integration of luminance-defined patterns [14, 18]) is neural integration of visual signals along the motion trajectory [16, 17, 19]. Given longer integration time for color signals than for luminance signals [20, 36], motion blur is a more severe problem for color perception. The present findings suggest that trajectory integration may also be present for color signals. This mechanism could be thought of as internally tracking a moving object, combining color information only from that object. Such a mechanism would make the visual system less sensitive to color changes within moving objects, as we observed. However, in the general case, in which objects move without changing color, the same mechanism would help us extract veridical color information without motion blur while maintaining a high signal-to-noise

ratio. In agreement with this idea, we also found motion-induced color segregation in which alternations of different colors at the same retinal location are more clearly segregated (i.e., less mixed) in moving patterns than in nonmoving patterns flickering at the same rate [37]. Considering these and other related findings [38–43], we conjecture that motion may generally play a role in guiding how patterns and colors are spatiotemporally bound to object representations.

Given that visual motion detectors do not exist before the visual cortex in humans, the effects of motion on color, along with dichoptic color mixing [44], suggests a significant contribution from cortical processing to color mixing, which is often considered to reflect earlier visual processes. In addition, indifference to the direction of color modulation of motion-induced color mixing can be interpreted as suggesting an involvement of cortical color mechanisms in which L-M and S chromatic signals are not segregated [45]. Burr and Ross [17, 19] suggested that trajectory integration of luminance-defined pattern signals may be mediated by directionally selective neurons having spatiotemporally oriented receptive fields [46], which are normally considered only as the mechanism for motion detection [47]. Similarly, the neural mechanism underlying motion-based color processing may be color-sensitive neurons having spatiotemporally oriented receptive fields. Some neurons in monkey V1 and V2 show dual selectivity to motion direction and color [48, 49]. The weakness of this suggestion, however, is that only a small proportion of visual neurons seem to have this property, whereas the perceptual phenomena are very robust against various changes in stimulus condition. Alternatively, the visual system may implement trajectory integration in a more global interaction between the motion-processing subsystem and the subsystems for processing color and other visual attributes. This possibility is consistent with general trajectory integration of various attributes, as well as involvement of high-level motion processing in trajectory integration [18].

Here, we show the evidence of motion-induced color mixing. This finding supports the notion of functional inseparability of visual attributes [50] and reveals a new role of motion signals in color perception. Integration of color signals along the motion trajectory is potentially a useful mechanism to see veridical colors of moving objects.

Experimental Procedures

Observers

Participants in each experiment were two or three of the authors and two to four volunteers unaware of the purpose of the experiments, all having normal or corrected-to-normal vision.

Apparatus

Stimuli were displayed on a GDM-F520 CRT monitor (Sony), with a refresh rate of 160 Hz, driven by a VSG2/5 visual stimulus generator (Cambridge Research Systems) installed in a Precision 350 workstation (Dell). The spatial resolution of the monitor was 800×600 pixels, with each pixel subtending 1.5 min at the viewing distance of 113 cm. The observer viewed the monitor while sitting in a dimly illuminated room with his or her head fixed on a chin rest.

Color Specification

A linear scale of color mixture was made by modulating the intensities of red (CIE (1931); $x = 0.625$, $y = 0.341$) and green ($x = 0.290$,

$y = 0.606$) phosphors. Two colors of a given red-green pair were $al_{red} + bl_{green}$, and $bl_{red} + al_{green}$ where l_x is full-contrast intensity of color x , $a > b$, and $a + b = 1$. The chromatic contrast, defined as $a - b$, was 100%, 75%, 50%, 25%, and 0% for M (mixture magnitude) = 1, 2, 3, 4, and 5, respectively. This gives rise to a pair of red and green for $M = 1$ (perfect segregation) and a pair of identical yellows for $M = 5$ (perfect mixture). Under the maxluminance condition, each phosphor was driven at maximum intensities of the monitor, at which point $M = 1$ ($l_{red} = 28 \text{ cd/m}^2$ and $l_{green} = 84 \text{ cd/m}^2$). Under the equiluminance condition, $l_{red} = 28 \text{ cd/m}^2$ and l_{green} was defined individually by means of flicker photometry [36]. The chromaticity of yellow varied depending on the luminance setting of l_{green} . For S axis modulation, a similar scale of color mixture was made between ($x = 0.409$, $y = 0.492$) and ($x = 0.233$, $y = 0.123$). The luminance was 30 cd/m^2 .

Rating

The color-alternating motion stimulus consisted of two arrays of bars (1° in height, 20° in width) presented on a dark background, 1.0° or 3.0° above and below the fixation marker located at the center of the display (Figure 1A). The bar width was variable between 3 to 12 min. The center-to-center separation between adjacent bars was 20 times the bar width. The bar arrays jumped every 6.25 ms (SOA), with a step equal to the bar width (Figure 1B), in opposite directions in the upper and lower arrays. At every jump, the color of all bars was synchronously changed between red and green (when $M = 1$ of the red-green condition). Repeat presentation of the bar always fell on a location that had carried the same color. The duration of a motion sequence was 200 ms (32 frames). For masking stimulus onset and offset, the first frame was presented in yellow from 3 s before a motion sequence, and the last frame was presented in yellow until 0.6 s after the sequence. Initial bar positions were randomized. The control flash stimulus (Figures 1C and 1D) consisted of color stripes containing ten bars separated by a blank of the same width. It flashed (single frame) twice with an interval of 125 ms, without a premask or postmask. In each trial, a stimulus presentation was followed by a presentation of a static color sample. The sample consisted of five pairs of colored bars showing five mixture magnitudes, and the observer had to choose the sample number closest to the impression of perceived colors. (Or, the color sample was bicolor bar arrays presented with one of five mixture magnitudes, and the observer varied the mixture magnitude to match sample colors to the perceived test colors. We confirmed that the results obtained with this “matching” procedure were not significantly different from those obtained with the “rating” procedure.) The observer could request replays of the stimulus sequence. Between trials within a single session, the stimulus type, bar width, color-mixture magnitude, and motion direction were randomly varied. Eccentricity and luminance conditions were varied between sessions.

Temporal parameters were changed when the SOA was a variable (Figure 3). Stimulus duration was 1 s (160 frames). At every constant interval of time (SOA), an updated image of bar arrays was presented in a single-monitor frame. A blank field with a fixation point was presented during the interval. The control stimulus was flashed twice with an interval of 500 ms.

Chromatic-Contrast Detection

In a single trial, a target of a given chromatic contrast and a nontarget of 0% contrast were simultaneously presented, one above and the other below fixation. The observer had to keep fixating at the central point during stimulus presentation, and then indicated the target position by pressing one of two buttons. The color condition was red-green equiluminance. Unless otherwise noted, other stimulus parameters were the same as those used for the rating experiments. The chromatic contrast was varied within a block, and the stimulus type (color-alternating motion [Figure 1B] or flash [Figure 1D]) and bar width (6, 9, or 12 min) were varied between blocks. Using the method of constant stimuli, we estimated the threshold chromatic contrast from the 75% correct point of the best-fit logistic function.

Supplemental Data

Supplemental Data include supplemental results and seven figures and are available with this article online at: <http://www.current-biology.com/cgi/content/full/17/4/366/DC1/>.

Acknowledgments

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Supplemental Data

Human Visual System Integrates Color Signals along a Motion Trajectory

S1

Shin'ya Nishida, Junji Watanabe, Ichiro Kuriki,
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Supplemental Results

Supplemental Data of Rating Experiments

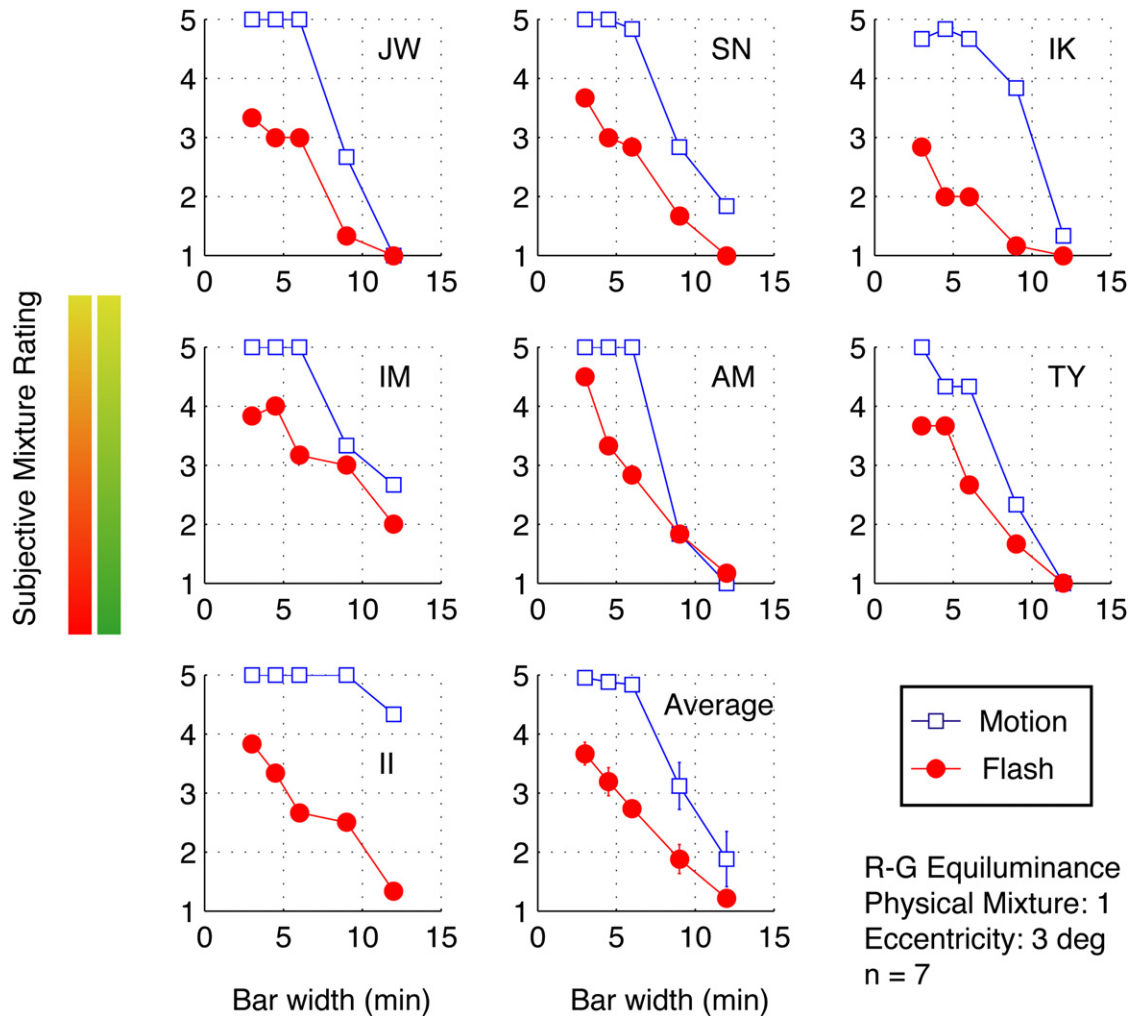


Figure S1. Individual Data of the Rating Experiment of Color Mixing

The corresponding group data is shown in Figure 2C. The effect of motion on color mixing is evident for all the seven observers. Error bars shown in the last panel (Average) indicate the standard error across observers.

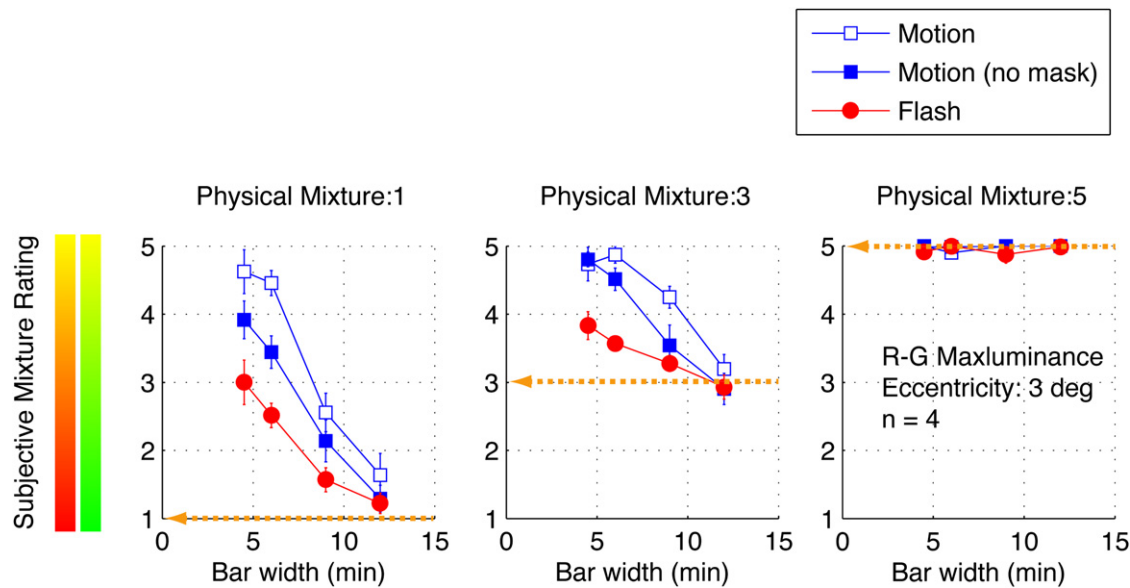


Figure S2. The Effect of Premasks and Postmasks on Motion-Induced Color Mixing

The color-mixture rating for the three stimulus conditions (motion with and without masks, and flash) was collected in the same session. Each data point shows the average for five observers (at least six judgments for each). Motion-induced color mixing was observed regardless of the mask condition, although the removal of the masks slightly lowered the mixture rating because of failure of color integration at stimulus onset and offset. Error bars indicate the standard error across observers.

Eye-Movement Artifacts

Here we consider eye-movement artifacts. If the observer's eyes tracked the stimulus movement despite our instruction to fixate at the center of the display, the colors along a motion trajectory would superimpose at the same retinal location. In that case, the conventional retinal color-integration mechanism could account for motion-induced color mixing. We tested the possible role of eye-movement artifacts in two additional experiments.

In one experiment, we measured eye movements while the observers performed the same tasks as in the main experiments. The eye movement was monitored by an infrared eye tracker (Iota Orbit 8, sampling rate: 1 kHz) while the observer performed the task similar to the main rating experiments. A session consisted of 24 trials for the motion stimulus (12 trials each for leftward/rightward and for rightward/leftward directions) and 24 trials for the control flash stimulus. The results (Figure S3) do not indicate such large eye movements as tracking the stimulus motion, nor significant differences between the stimulus conditions. At a closer look, in some trials, the eye position shifted ~ 10 min during a 200 ms presentation of a color-alternating stimulus. However, it is unlikely that this eye movement generated motion-induced color mixing. First, color-mixture rating for motion stimuli was always 5 (indicated by red line), regardless of the magnitude of eye movement, which varied from trial to trial. Second, the rating results (Figure 2) suggest that mixture ratings for 6 min moving bars were comparable to, or slightly higher than, those for 3 min flashing bars. One way to interpret this result is that the effect of motion on color mixture (in this specific case) is equivalent to doubling the apparent spatial frequency of the stimulus. The speed of following eye movements required to double the spatial frequency of the retinally

painted pattern of the color-alternating moving stimulus is half of the stimulus speed (i.e., 96 min/200 ms). This is much higher than we observed. Another, and more conservative, estimation of the following eye speed to account for the rating results is a quarter of the stimulus speed (i.e., 48 min/200 ms), at which each 6-min-width bar will have a 3 min area free from retinal color overlap. This estimation is still much higher than we observed.

In the other experiment, we used psychophysical tests to evaluate the contribution of any form of eye movement, including small involuntary ones, to color mixing (Figure S4). If colors are mixed in the color-alternating motion stimulus as a result of eye movements, colors will be similarly mixed in a simultaneously presented stationary-color-stripe pattern, and colors will be segregated in the simultaneously presented stationary-counterphase-color-stripe pattern. These possibilities were tested by simultaneous presentation of two different stimulus patterns in a single trial. The method was the same as those used in the main rating experiments except for the following points. In a single trial, two stimulus patterns were simultaneously presented only once, one above and the other below fixation. The observer rated the magnitude of color mixture first for the upper pattern and then for the lower one, on the basis of visual memory. Therefore, the pattern of eye movements should have been always the same for the two stimuli. The positions of moving and control stimuli were exchanged between sessions. The stationary and counterphase stripes had the same spatial structure as the flash control stimulus for color mixing, but were continuously presented for 200 ms as a stationary pattern, or with the spatial phase reversed every 6.25 ms. The results show that whereas the color mixture ratings for the color-alternating motion pattern remained nearly the same as those in Figure 2B, colors were clearly

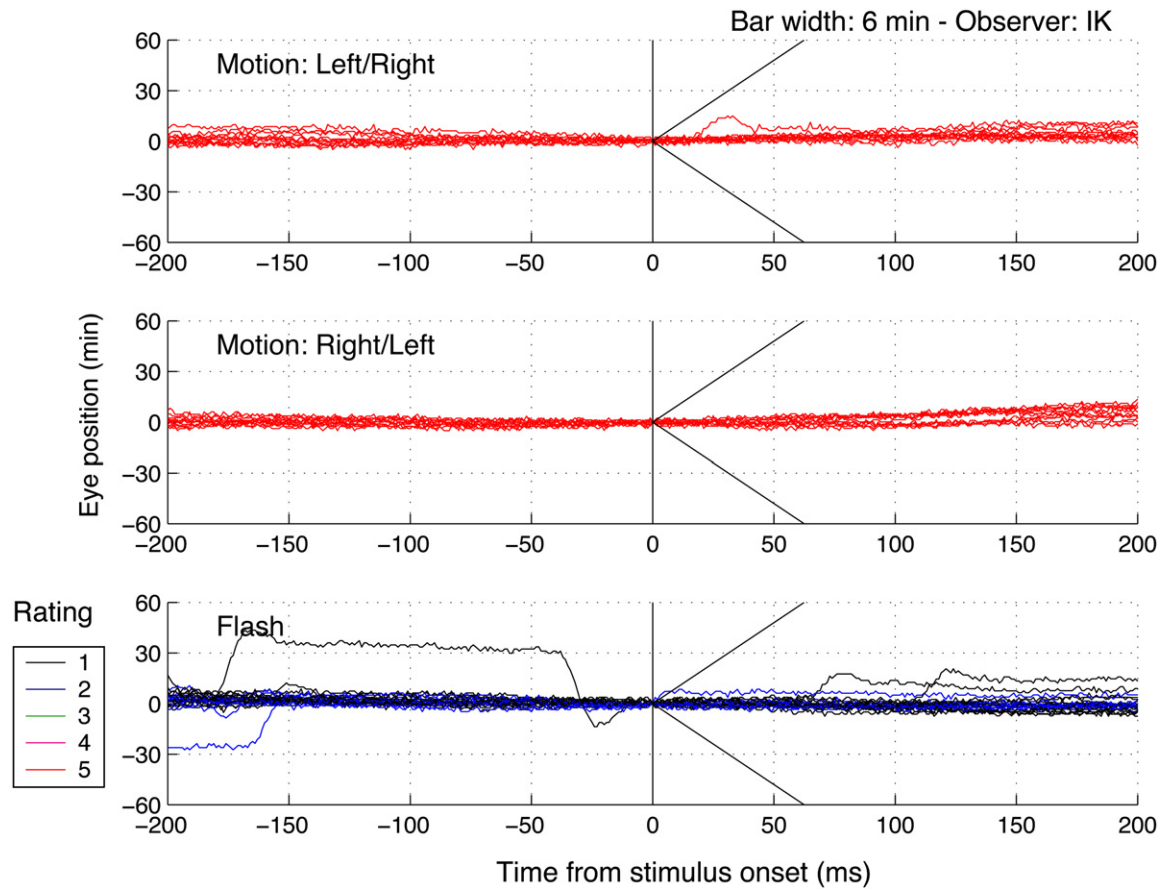


Figure S3. Eye-Movement Measurement during Motion-Induced Color Mixing

Separately for the three stimulus conditions, the horizontal position of the left eye measured in each trial is plotted as a function of time, with the color of the line indicating the rating of color mixing in the trial. The stimulus presentation started at time = 0. Diagonal lines indicate the trajectories of stimulus movements. The results are of one observer, but similar results were obtained for the second observer.

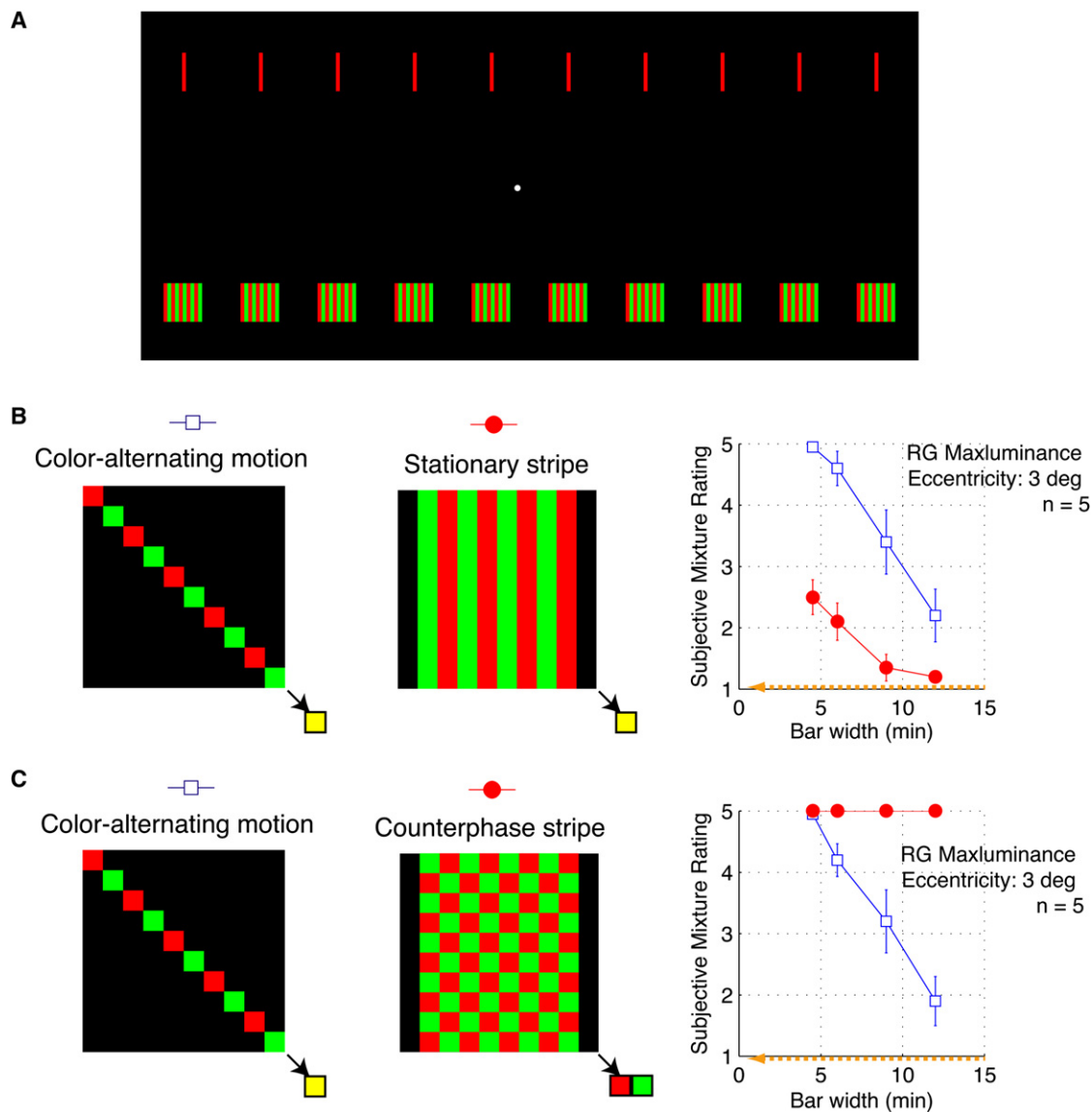


Figure S4. Psychophysical Tests for Eye-Movement Artifacts

(A) Motion and stationary stimuli were simultaneously presented.

(B) Presentation of the color-alternating motion stimulus for color mixing (Figure 1B) with a stationary-stripe pattern.

(C) Presentation of the color-alternating motion stimulus with a counterphase-stripe pattern.

The results do not indicate the predicted changes that should occur in color perception in the stationary stimuli (colors indicated by arrows) if eye movements caused motion-induced color mixing. Each point shows the average for five observers (six judgments for each). Error bars indicate the standard error across observers.

segregated in the stationary color stripe and perfectly mixed in the counterphase stripe. These results indicate that motion-based color mixing cannot be ascribed to any kind of eye-movement artifacts.

Optical-Blur Artifacts

Here we argue against the criticism that motion-induced color mixing that prefers narrow bars might be ascribed to retinal-image degradation caused by physical blur on the display or by optical blur due to accommodation error or chromatic aberrations in an observer's eyes.

Although we do not exclude optical blurs as a cause of apparent color mixing in our experiments, they are expected to affect moving and control (flashing or stationary) stimuli in a similar fashion (especially when

they were presented at the same time; Figure S4) and thus unlikely to produce their differences in color perception. At long SOAs, motion-induced color mixing is observed even for wide bars (Figure 3). We had also observed that apparent color mixing seen for narrow bars was significantly weakened when the strength of perceived motion was reduced by prolonged presentation of the same stimulus for tens of seconds (motion adaptation) or by having observers see only a portion of moving trajectory through a slit of the width of several bars.

Inspection of presented images indicated that display blur is never so large that it would give rise to nearly perfect mixing for moving stimuli of the minimum bar width (2 pixels). To further check the display-blur artifact, we

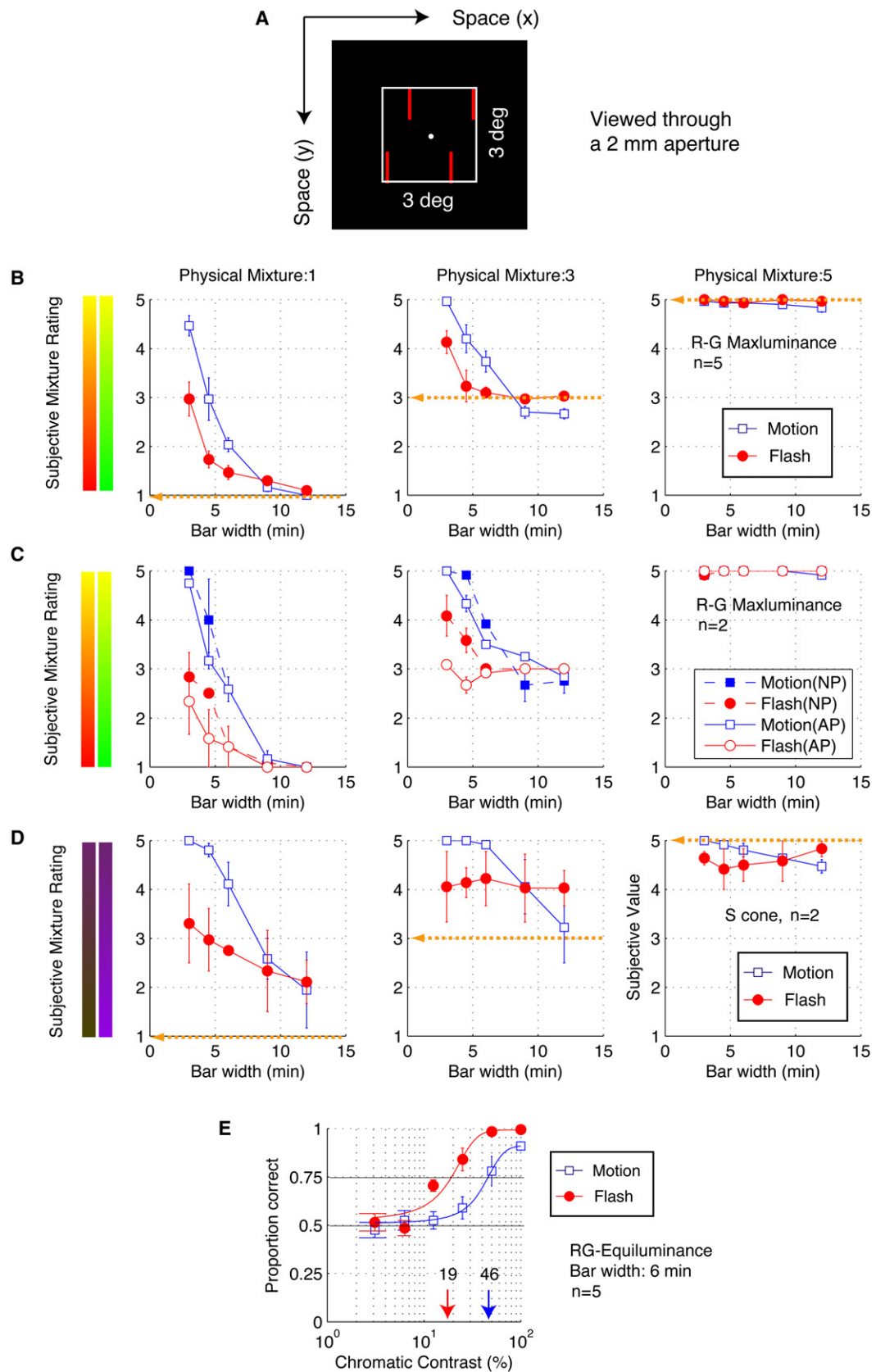


Figure S5. A Series of Experiments for Testing Chromatic-Aberration Artifacts

(A) We presented 1-degree-eccentricity stimuli only in the central 3×3 degree area (indicated by a white square, which was not included in the actual stimulus). The control stimuli were presented with no spatial blank. SOA was 6.25 ms. Observers monocularly viewed the stimulus through

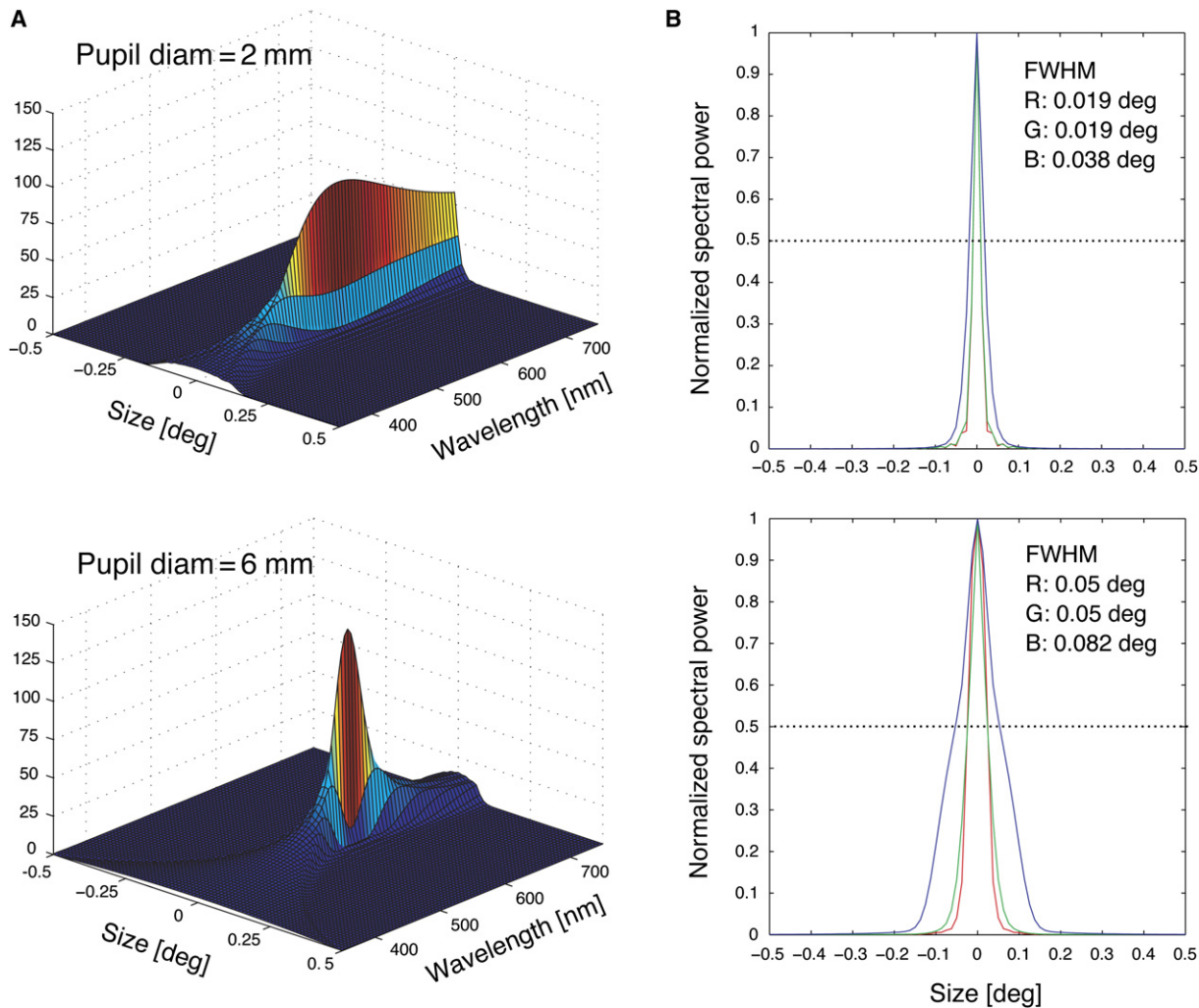


Figure S6. Estimation of the Optical Blur Arising from Longitudinal Chromatic Aberrations

We used formulas provided by Marimont and Wandell [S1].

(A) Line-spread functions illustrated in the same format as Figure 4 in [S1], calculated with 2 mm pupil diameter (top) and 6 mm pupil diameter (bottom).

(B) Profile of line-spread function of R, G, and B phosphors, calculated from the estimated line-spread function and the spectral-power distribution of each phosphor. These line-spread functions show that small pupil diameter is effective in suppressing blur at the retina. The full widths at half maximum (FWHM) for blurs of red and green phosphors were about 0.019 degrees under the 2-mm-pupil-diameter condition and about 0.05 degrees under the 6-mm-pupil-diameter condition. In agreement with this significant reduction of optical defocus, the results of an additional experiment suggest that the use of artificial aperture reduces overall mixture ratings (Figure S5). Nevertheless, the use of aperture had little effect on the magnitude of motion influence on apparent color mixing.

The use of an artificial pupil does not reduce wavelength-dependent lateral displacements of retinal image, known as transverse chromatic aberration. The direction of displacements by optical aberration is basically circularly symmetric around the optical axis. Therefore, if motion-induced color mixing is a result of this optical distortion, it should show some spatial inhomogeneity across the stimulus display. However, we have never met such a circularly asymmetric distortion in the perception of motion-induced color mixing at either 1 or 3 degrees eccentricity.

a small artificial pupil (2 mm in diameter) placed in front of their dominant eye. We expected that this viewing condition should significantly reduce optical blur arising from chromatic aberration (see Figure S6).

(B) The results of a rating experiment for motion-induced color mixing obtained with the aperture-viewing and RG-maxluminance stimuli. The effect of motion remained to be observed.

(C) The magnitude of the effect of motion appeared to be somewhat reduced with an artificial aperture (AP) in (B) as compared to the data collected with natural pupils (NP) at the same eccentricity in the main experiment (Figure 2A). However, the comparison of the two experiments is complicated by the fact that we reduced the stimulus-array width (which could degrade the perceived motion) and used a different set of observers. We therefore compared the ratings obtained with and without the aperture by using the same stimulus configuration (A) and observers. The results suggest that the artificial aperture reduces overall mixture ratings, but has little effect on the magnitude of motion influence on apparent color mixing.

(D) The results of a rating experiment with the aperture-viewing and S cone-modulation stimuli. Figure 2D shows the results of a comparable condition with natural pupils.

(E) The chromatic-contrast-detection performance. Figure 4 shows the results of comparable conditions (but measured at 3 degree eccentricity). The magnitude of the induction effect evaluated in terms of threshold chromatic-contrast ratio was comparable to those of the original experiments (2.4 versus 1.7–3.5). These results argue against the hypothesis that chromatic aberration is a main cause of motion-induced color mixing. Error bars indicate the standard error across observers.

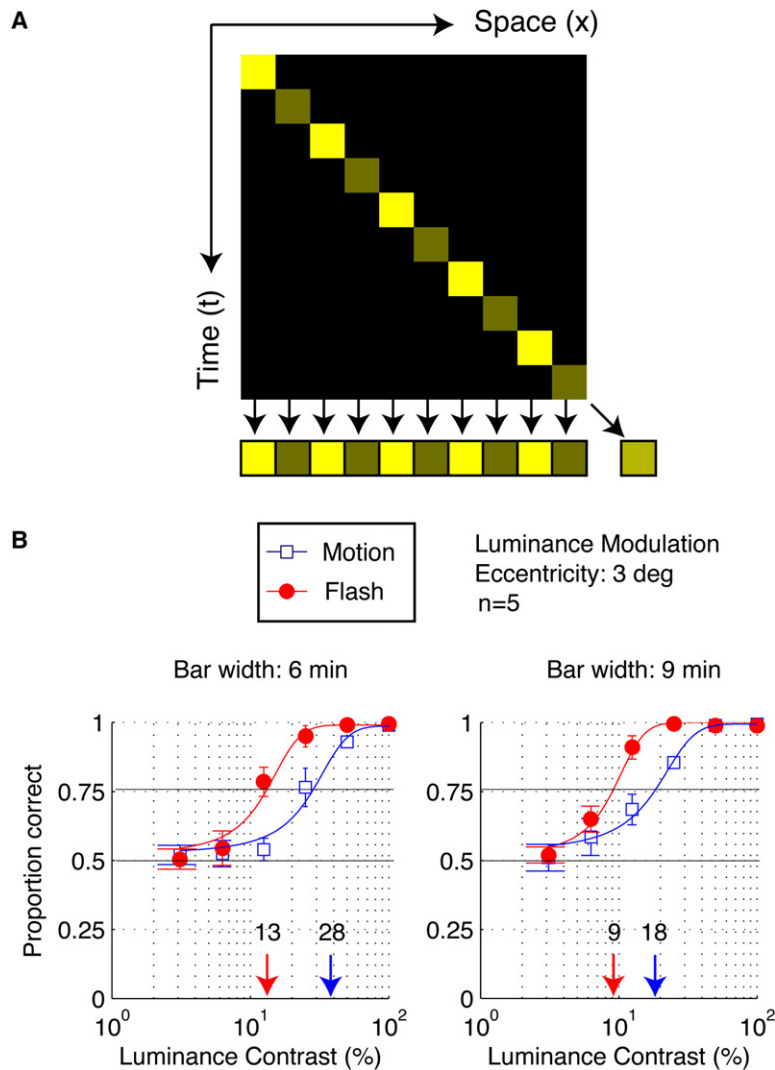


Figure S7. Motion-Based Intensity Mixing

(A) The stimulus was an achromatic version of the color-alternating motion stimulus, in which dark and bright yellow bars alternatively appeared along motion trajectories. According to our hypothesis that the visual system integrates sensory signals arising from the same moving object, similar perceptual fusion along motion trajectories will also occur for other properties including intensity. However, if motion-induced color mixing is merely an artifact of chromatic aberration, motion-induced intensity mixing will not occur. Phenomenologically, the luminance-alternating motion stimulus often appeared to move without intensity changes, suggesting the occurrence of motion-induced luminance mixing.

(B) To validate this observation, we measured the luminance-contrast-detection threshold for moving and control flashing stimuli. We asked observers to discriminate two stimuli of the same mean luminance, one with and the other without luminance modulations. The procedure was similar to that of the chromatic-contrast-detection experiment (Figure 4). The results indicate that luminance modulation was harder to detect in moving stimuli than in flashing stimuli, as we expected.

Error bars indicate the standard error across observers.

made the stimuli four times larger on the cathode-ray tube (CRT) and viewed them at the distance four times longer. Under this viewing condition, the stimuli on the retinal image should be similar to the original ones, except for a significant reduction of the display blur. Nevertheless, we could still observe phenomena similar to those observed under the original viewing condition. This indicates that display blur had no critical influence on our findings.

To further check the chromatic-aberration artifact, we conducted two additional experiments. In one experiment (Figure S5), we had observers monocularly view the stimuli through a small artificial pupil (2 mm in diameter) placed in front of their dominant eye, thus confining stimulus presentation in the central visual area. This viewing condition is expected to significantly reduce optical blur arising from chromatic aberration (Figure S6). Nevertheless, we could still observe motion-induced color mixing.

In another experiment (Figure S7), we found the occurrence of motion-induced signal mixing not only for chromatic stimuli, but also for achromatic stimuli. That is, apparent mixing of stimulus intensity was observed

for an achromatic version of the color-alternating motion stimulus in which dark and bright yellow bars alternatively appeared along motion trajectories. Although this result is consistent with our hypothesis that the visual system generally integrates sensory signals arising from the same moving object, it cannot be explained by the hypothesis that motion-induced mixing is merely an artifact of chromatic aberration.

Supplemental References

- S1. Marimont, D.H., and Wandell, B.A. (1994). Matching color images: The effects of axial chromatic aberration. *J. Opt. Soc. Am. A* 11, 3113–3122.