An expansive, cone-specific nonlinearity enabling the luminance motion system to process color-defined motion

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To conclude that there is a dedicated color motion system, the hypothesis that the luminance motion pathway is processing color motion due to some nonlinearity must be rejected. Many types of nonlinearities have been considered. Cavanagh and Anstis (1991) considered interunit variability in equiluminance, but they found that adding a color-defined modulation to a luminance-defined drifting modulation increased the contribution to motion. This color contribution to motion cannot be due to interunit variability in equiluminance alone because such a luminance artifact would increase the effective luminance contrast for some luminance-sensitive units and decrease it for the others, resulting in no additional contribution to motion on average. Cavanagh and Anstis considered this color contribution to motion as evidence of a dedicated color motion system, but here we show that such a color contribution to motion varies with the phase difference between the luminance and color modulations, which would not be expected if luminance- and color-defined motion were processed separately. Specifically, the contribution to motion was greater when the luminance and color modulations were aligned (i.e., 0° or 180° phase difference), than when they were not (90° or 270° phase difference). Such a luminance-color phase interaction was also observed when spatially interleaving luminance and color information, which suggests that the interaction occurs after some spatial integration (i.e., not at the photoreceptors). To our knowledge, this luminance-color phase interaction cannot be explained by any previously considered nonlinearity. However, it can be explained by an expansive nonlinearity occurring before the summation of the L- and M-cone pathways (i.e., before ganglion cells) and after some spatial integration (i.e., after the photoreceptors). We conclude that there is a nonlinearity that has not been considered before, enabling some color motion processing by the luminance motion system.

Introduction

Despite more than three decades of investigation, the existence of a dedicated color motion system distinct from both the luminance and feature tracking motion systems remains debated. Many consider it as well established (e.g., for reviews see Burr & Thompson, 2011; Cropper & Derrington, 1996; Cropper & Wuerger, 2005; Dobkins & Albright, 1993, 1994; Dougherty, Press, & Wandell, 1999; Gegenfurtner & Hawken, 1996; Hawken, Gegenfurtner, & Tang, 1994; McKeefry, Laviers, & McGraw, 2006; Nishida, 2011; Thiele, Dobkins, & Albright, 2001), but some argue against its existence (e.g., Lu, Lesmes, & Sperling, 1999; Mullen, Yoshizawa, & Baker Jr, 2003). It is clear that under some conditions (e.g., high temporal frequencies) color motion cannot be processed by the feature tracking motion system and therefore must be processed by a low-level, energy-based motion system. This motion system could be a dedicated color motion system or the luminance motion system processing luminance artifacts due to some nonlinearity within the luminance pathway. Many nonlinearities (e.g., interunit variability in equi-luminance, temporal phase-lag between the processing of L and M cones, optical chromatic aberrations, and second harmonic) have been considered and were often found to be too weak to explain the color contribution to motion, which suggests the existence of a dedicated color motion system. However, the present study reveals the existence of some nonlinearity that, to our knowledge, have not been considered before and that enables the luminance motion system to process some color-defined motion.

To prevent the luminance motion system to process color-defined motion, color-defined motion is usually presented at equiluminance. However, interunit variability in equiluminance across luminance-sensitive
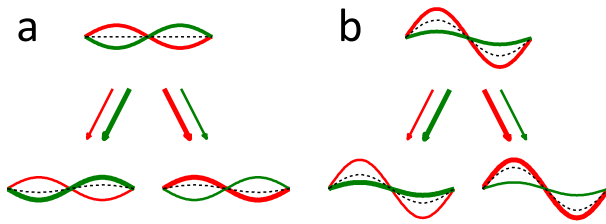
Figure 1. Impact of interunit variability in equiluminance for color-defined modulations. Red and green curves represent the luminance profile for L and M cones, respectively. Dash lines represent the mean luminance profile. (a) At equiluminance, units attributing more weight to either L or M cones (bottom-right or bottom-left, respectively) would introduce luminance modulations of opposite phases. (b) In the presence of a high contrast luminance modulation, attributing more weight to either L or M cones (bottom-right or bottom-left, respectively) would increase the effective luminance contrast for some units and decrease it for others resulting in no net gain on average.

motion units makes it impossible to have an equiluminant signal (i.e., no luminance modulation) simultaneously for all luminance-sensitive motion units (e.g., Logothetis, Schiller, Charles, & Hurlbert, 1990). Nonetheless, just because there must be some residual luminance-defined motion does not necessarily explain the color motion processing, as there could be a dedicated color motion system more sensitive to the color motion than the luminance motion system is sensitive to the residual luminance-defined motion.

Cavanagh and Anstis (1991) conducted a clever experiment to test if the color contribution to motion can be explained by interunit variability in equiluminance. The logic was that a color-defined signal at "equiluminance" (i.e., the strength of the red and green opposite modulations adjusted to minimize luminance-defined motion within the luminance pathway) corresponds to a luminance modulation of one polarity for luminance-sensitive motion units attributing more weight to L cones (Figure 1a, bottom-right) and to a luminance modulation of the opposite polarity for the ones attributing more weight to M cones (Figure 1a, bottom-left). By superimposing a high contrast luminance modulation to the color modulation (Figure 1b, top), the impact of interunit variability in equiluminance should become negligible because the variability in luminance modulations of different polarities due to the interunit variability in equiluminance would sum with the superimposed luminance modulation for some units (e.g., Figure 1b bottom-right) and subtract with others (e.g., Figure 1b bottom-left) resulting in no or little gain on average (Figure 2, dashed line). Since the color contribution to motion did not converge to zero when adding a luminance modulation to the color modulation (Cavanagh and Anstis, 1991 and illustrated by solid line in Figure 2), the color contribution to motion could not
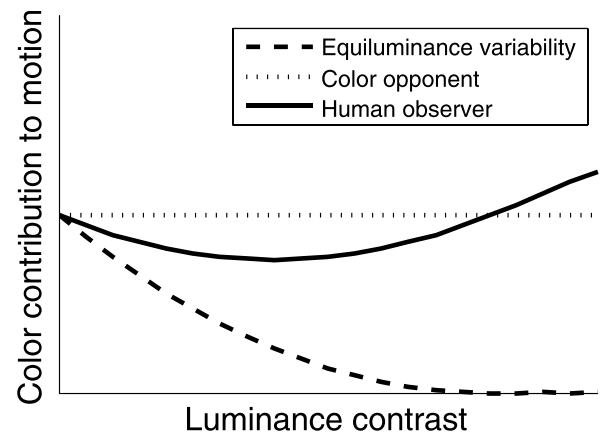

Figure 2. Color contribution as a function of the luminance contrast. If the color contribution to motion was due to interunit variability in the equiluminance (dashed line), then it should decrease with luminance contrast as shown here (see also figure 20 bottom-left of Cavanagh and Anstis, 1991). If it was due to a distinct color motion system, then it would likely be independent as illustrated by the dotted line (also illustrated in figure 22 of Cavanagh and Anstis, 1991). The solid line illustrates the empirical results obtained by Cavanagh and Anstis (figure 22, 1991): The color contribution to motion initially dropped and then increased with luminance contrast.

be solely explained by interunit variability in equiluminance. Cavanagh and Anstis (1991) considered this as evidence of a dedicated color motion system.

The target of the current study was to determine whether the color contribution to motion of superimposed luminance and color modulations reflects the existence of a dedicated color motion system or the combination of interunit variability in equiluminance and another unknown nonlinearity causing the color contribution to motion to increase with luminance contrast (Figure 3). To investigate which motion system is responsible for this color contribution to motion, we applied the phase dependence test (Lu & Sperling, 1995). If the color contribution to motion is due to a dedicated color motion system, then the color contribution to motion should be independent of the luminance-color phase difference. If some color contribution to motion were due to a multiplicative luminance artifact (i.e., artifact that increases with the luminance contrast), then such a phase interaction would likely occur.

Experiment 1: Phase-dependent test

The objective of the first experiment was to evaluate the contribution to motion of a signal composed of
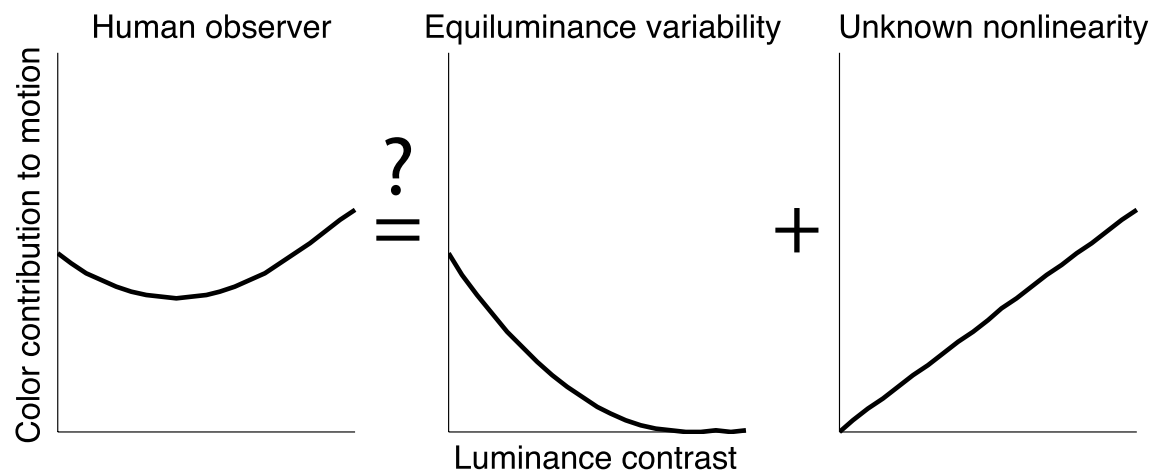
Figure 3. Color contribution to motion observed by Cavanagh and Anstis (1991, illustrated in the left graph) could be due to a combination of two factors: interunit variability in equiluminance (center graph) and another unknown nonlinearity causing the color contribution to motion to increase with luminance contrast (right graph).

superimposed luminance- and color-defined drifting modulations as a function of their phase difference (Figure 4). The contribution to motion of combined modulations was measured by opposing a luminance motion signal and adjusting its contrast until no net motion was perceived (Cavanagh & Anstis, 1991). When no net motion was perceived, the contribution to motion of the combined luminance- and color-defined drifting modulations was equivalent to the opposing luminance motion signal. The color contribution to motion was defined as the contrast difference between the two opposing luminance motion modulations when no net motion was perceived.

Method

Observers

One naïve observer and one of the authors participated in this experiment. They had normal or corrected-to-normal vision.

Apparatus

The stimuli were presented on a 19-inch CRT monitor with a refresh rate of 120 Hz using only the red and green guns. The Noisy-Bit method (Allard & Faubert, 2008) implemented independently to each gun made the 8-bit display perceptually equivalent to an analog display having a continuous luminance resolution. The monitor was the only source of light in the room. A Minolta CS100 photometer interfaced with a homemade program calibrated the output intensity of each gun. At the viewing distance of 114 cm, the width and height of each pixel were 1/64° of visual angle.

Stimuli and procedure

Stimuli were composed of three superimposed vertical sine wave modulations of 0.7 cpd, avoiding the potential influence of nonlinearities induced by transverse chromatic aberrations (Faubert, Bilodeau, & Simonet, 2000), and drifting at 7.5 Hz. Two modulations were defined by luminance and one by color (i.e., with the red and green modulations in phase and in opposite phase, respectively). The blue gun was never modulated and was set to the minimal intensity. Note that following Cavanagh & Anstis (1991), the color-defined modulation was defined as the opposite luminance modulations of the red and green color gun, not in cone contrast modulations of L and M cones. Nonetheless, given that the motion contribution of S
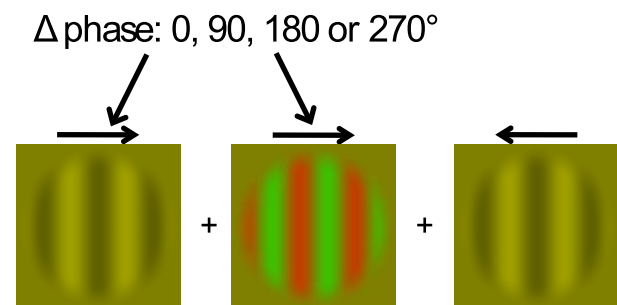

Figure 4. Stimuli were composed of three modulations: a color modulation (center) drifting in one direction and two luminance modulations drifting in opposite directions (left and right). The phase difference between the luminance and color modulations drifting in the same direction was systematically varied (phase-dependent test). The color contribution to motion was defined as the contrast difference between the two opposing luminance motion signals when no net motion was perceived.

cones is weak (e.g., Lee & Stromeyer, 1989; Wandell et al., 1999), we assumed that the contribution to motion of S cones was negligible and the contribution to motion was therefore due to L and M cones (L + M or L - M).

To avoid luminance-color interaction due to monitor nonlinearity, the luminance and color modulations were temporally interleaved at 60 Hz (e.g., even frame contained only the color-defined modulation and odd frames contained only luminance-defined modulations). One luminance-defined modulation was drifting with the color-defined modulation (i.e., in the same direction) and the other was drifting in the opposite direction. The contrast of the color-defined modulation was fixed to 12.5% contrast (i.e., the contrast of the red and green modulations were both fixed to 25% in "color" frames and to 0% in "luminance" frames). The drifting direction (left or right) and initial phase of the color-defined modulation were both randomized on each trial. The contrast of the luminance-defined modulation drifting with the color-defined modulation was fixed to 0%, 2.5%, 5%, 10%, 20% or 40% of the color modulation contrast. Since the luminance contrast relative to the color contrast is more relevant than the absolute luminance contrast (and for comparative reason with previous findings, Cavanagh & Anstis, 1991), the present study reports all luminance contrasts relative to the color-defined modulation contrast. The luminance-color phase difference was 0°, 90°, 180° or 270° (0° difference corresponds to the luminance-defined modulation aligned with the red modulation of the color-defined modulation). The opposing luminance-defined modulation had a randomized initial phase and its contrast was controlled by a 1-down-1-up staircase procedure (Levitt, 1971) of 200 trials with 0.05 log steps, which converged to the contrast at which no net motion was perceived. Specifically, in a 2AFC procedure (left or right), the contrast was increased or decreased depending on whether the observer judged the net motion to be in the opposite or same direction, respectively, to the luminance modulation controlled by the staircase procedure.

There were six blocks of trials (one for each luminance contrast) containing each four staircases that were pseudo randomly interlaced for the four luminance-color phase differences (except for the 0% luminance contrast which had only one staircase as there was no luminance-color phase difference). Observers were asked to fixate the black dot presented in the middle of the screen and report the net moving direction (left or right). The spatial window was 2.8° wide plus half-cosine smooth edges of 0.5°. The presentation time was 250 ms plus an onset and offset half cosine ramp of 125 ms.

To minimize luminance-defined motion within the luminance pathway, the mean luminances of L and M responses were perceptually equated independently for each observer. Otherwise, a "color-defined" modulation would contain a luminance modulation matched in phase or in opposite phase. Such a luminance artifact would interact with the superimposed luminance-defined modulation drifting with the color-defined modulation. This artifact would increase or decrease the motion strength in the direction of the color-defined modulation so that a higher or lower luminance contrast would be required in the opposite direction to cancel the combination of luminance and color motion depending on whether the luminance-color phase difference is 0° or 180°. To minimize such artifacts, the relative mean luminances of the red and green guns were equated. The mean luminance of the red gun was fixed to 50% of the maximum red luminance and the mean luminance of the green gun was adjusted based on a pilot experiment for each observer and each block of trials (i.e., for each luminance contrast) to 14% and 10% of the maximum green luminance, respectively. This adjustment resulted in a background CIE x, y coordinate of (0.415, 0.391) and (0.422, 0.378), and a mean luminance of 17.2 and 15.5 cd/m^2, for observers IL and RA respectively. Note that the similar color contributions to motion observed for the 0° and 180° luminance-color phase difference (see Results section) confirms that the L and M cone responses were roughly equated on average.

Another nonlinearity that introduces a luminance artifact within the color-defined modulation is the different phase-lags between the processing of the L and M cones. Indeed, M cone processing is slower (e.g., Cushman & Levinson, 1983) and this delay introduces a luminance artifact offset by 90° from the color-defined modulation, which would interact with the luminance-defined modulation drifting with the color-defined modulation. This artifact will increase or decrease the motion strength in the direction of the color-defined modulation so that a higher or lower luminance contrast will be required in the opposite direction to cancel the combination of luminance- and color-defined motion depending on whether the luminance-color phase difference is 90° or 270°. To compensate for this phase-lag, a temporal offset was introduced between the modulations of the red and green guns based on a pilot experiment for each observers and each block of trials (i.e., for each luminance contrast). The modulations of the red gun preceded the ones of the green gun by a phase angle of about 0.20° and 0.33° for observers IL and RA, respectively. Note that the similar color contribution to motion observed for the 90° and 270° luminance-color phase difference (see Results section) confirms that the phase-lag difference for L and M cone responses were compensated for.
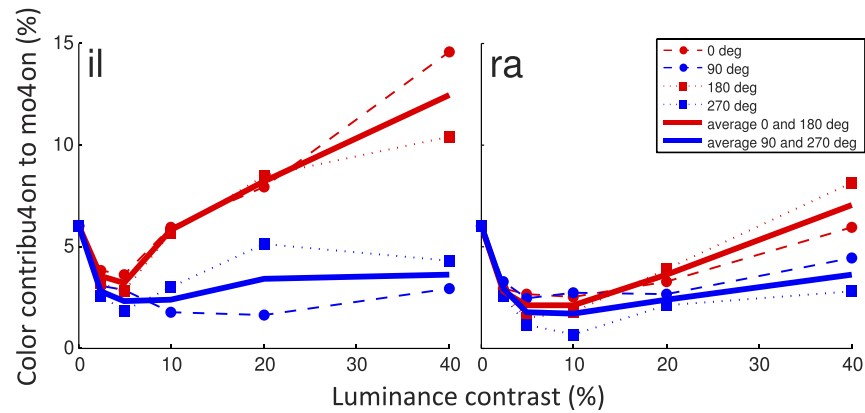
Figure 5. Color contribution to motion as a function of luminance contrast for 4 luminance-color phase differences (0°, 90°, 180° and 270°). Solid lines represent mean color contribution to motion when luminance and color modulations were aligned (i.e., 0° and 180°, red lines) and offset by 90° (i.e., 90° and 270°, blue lines).

Results and discussion

As shown in Figure 5, when the luminance and color modulations were aligned (0° and 180° differences, red dashed and dotted lines, respectively), the color contribution to motion dropped with luminance contrast at low luminance contrast, but rose at high luminance contrast. This pattern of results is consistent with previous findings (Cavanagh & Anstis, 1991) illustrated by the solid line in Figure 2, which cannot be explained by an additive luminance artifact (i.e., contrast of the luminance artifact independent of the contrast of the luminance-defined modulation) of the same spatiotemporal frequency as the color-defined modulation. Indeed, such an additive luminance artifact would interact with the luminance-defined modulation by increasing its effective contrast for a given phase and decreasing it for the opposite phase resulting in no net gain on average. The fact that the mean color contribution to motion of these two opposite luminance-color phase differences (Figure 5, red solid line) was substantially above zero implies that the color contribution to motion cannot be solely explained by an additive luminance artifact of the same spatiotemporal frequency as the color-defined modulation as argued by Cavanagh and Anstis (1991).

When the luminance and color modulations were out of phase (90° and 270° differences), the rising portion of the curve at high luminance contrast was less pronounced: The color contribution to motion was weaker. Given that the phase information is lost at the motion extraction stage, this phase interaction cannot be explained by an independent color motion pathway and suggests the existence of some nonlinearity within the luminance pathway before the motion extraction stage. Furthermore, nonlinearities *after* the summation of the L and M pathways would not cause any strong luminance-color phase interaction or any strong color

contribution to motion at high luminance contrast because any color information of opposite polarities between the L and M cones would be lost (or substantially reduced) at this stage. Cavanagh and Anstis (1991) illustrated this outcome by simulating a nonlinear contrast response within the luminance pathway, after the merging of the L and M pathways. A strong compressive or expansive contrast response (e.g., contrast response proportional to the square root or square of the stimulus contrast, respectively) would not result in a strong color contribution to motion at high luminance contrast (figure 20 of Cavanagh & Anstis, 1991). This suggests that the nonlinearity responsible for the luminance-color phase interaction occurs *before* the merging of the L and M pathways.

Experiment 2: Luminance harmonic artifacts?

The color contribution to motion in the presence of a high contrast luminance modulation in the previous experiment cannot be explained by an additive luminance artifact of the same spatiotemporal frequency as the color-defined modulation. In the second experiment, we consider additive luminance artifacts of a *different* spatiotemporal frequency. Early distortions (e.g., at the photoreceptor level) could introduce luminance harmonics (Derrington, Krauskopf, & Lennie, 1984; Schiller & Colby, 1983). The second harmonic is particularly interesting because it has a spatial and a temporal frequency twice those of the color modulation, so when shifting the color-luminance phase difference by 180°, the second harmonic is shifted by 360°. This frequency doubling could explain the similar results obtained between the 0° and 180°, and

between the 90° and 270° color-luminance phase difference, as well as the difference between these two groups if there is a substantial phase interaction between the processing of a luminance modulation and another luminance modulation that has twice its spatial and temporal frequency (i.e., second harmonic).

Nevertheless, it is unlikely that a second harmonic could cause both the rising color contribution to motion with the luminance contrast and the luminance-color phase interaction. Indeed, the contribution to motion of a second harmonic would not be expected to depend on the phase relation with the fundamental luminance modulation and would not be expected to increase with the luminance contrast of the fundamental luminance modulation. However, to ensure that the second harmonic artifacts were too weak to substantially contribute to motion, the current experiment measured their strength using a quadrature phase procedure similar to the one used by Cavanagh and Anstis (1991).

Method

The stimuli were composed of the sum of two color-defined modulations and two luminance-defined modulations. The color-defined modulations were identical to the ones in the previous experiment (i.e., 12.5% contrast, 7.5 Hz, 0.7 cpd and randomized initial phase) and were drifting in opposite directions. The two luminance-defined modulations had a spatial and temporal frequency twice the one of the color-defined modulations (i.e., 1.4 cpd and 15 Hz) and were also drifting in opposite directions. In one direction (randomly either left or right), the peaks of the luminance modulation were aligned with the peaks and troughs of the color-defined modulation and the contrast of the luminance modulation was fixed to 5% of the color contrast. In the opposite direction, it was the troughs that were aligned with the peaks and troughs of the color-defined modulation and the contrast of the luminance modulation was controlled by a 1-down-1-up staircase procedure as in the previous experiment, which converged to the contrast at which no net motion was perceived. If the color-defined modulation were converted into a second luminance harmonic, this harmonic would sum with one of the luminance modulations and subtract with the other, thereby increasing the motion response in one direction and reducing it in the other. If the luminance modulation plus the second luminance harmonic artifact had the same motion strength as the luminance modulation minus the second luminance harmonic artifact, then no net motion would be perceived. It is therefore possible to measure the harmonic of the visual system, which is equal to half of the difference between the contrasts of the two luminance-defined modulations.

Results and discussion

Second harmonics were found to be less than 1% of the color modulation for both observers, which is consistent with previous findings (Cavanagh & Anstis, 1991). This second harmonic contribution to motion is much lower than the 8% color contribution observed in the first experiment and is too low to generate a motion sensation by itself in the testing conditions of Experiment 1. These results suggest that the color contribution to motion was not due to an early nonlinearity introducing a second harmonic luminance artifact.

Given that the contrast of the harmonics are expected to decrease with the harmonic order and that the human sensitivity to any harmonic above the second harmonic (e.g., the third harmonic is a 2.1 cpd signal drifting at 24 Hz) is very low, we conclude that the color contribution to motion observed in the previous experiment is not due to an additive luminance artifact at a frequency different from the one of the color-defined modulation. Thus, taken together, the results of the first two experiments cannot be explained by an additive luminance artifact (i.e., with a contrast that depends only on the color-defined modulation, not on the luminance-defined modulation).

Experiment 3: Origin of the nonlinearity

Given that information from L and M cones merges at the ganglion cell levels (either by summing or subtracting resulting in the luminance or color pathways, respectively), the results of the first experiment suggest that the luminance-color phase interaction occurs earlier, that is, either at the photoreceptor or bipolar cell levels. Both of these levels process information from L and M cones separately, but an important distinction between the two is the size of their receptive fields. Photoreceptors have small receptive fields and bipolar cells have large center-surround receptive fields as they integrate information over many photoreceptors via horizontal cells. The target of the third experiment was to determine whether the phase interaction between luminance and color processing occurs before (e.g., photoreceptors) or after (e.g., bipolar cells) a substantial spatial integration. To test these hypotheses, the luminance-color phase interaction was evaluated when spatially interleaving the luminance and color information at a high spatial frequency (Figure 6). On the one hand, if the luminance-color
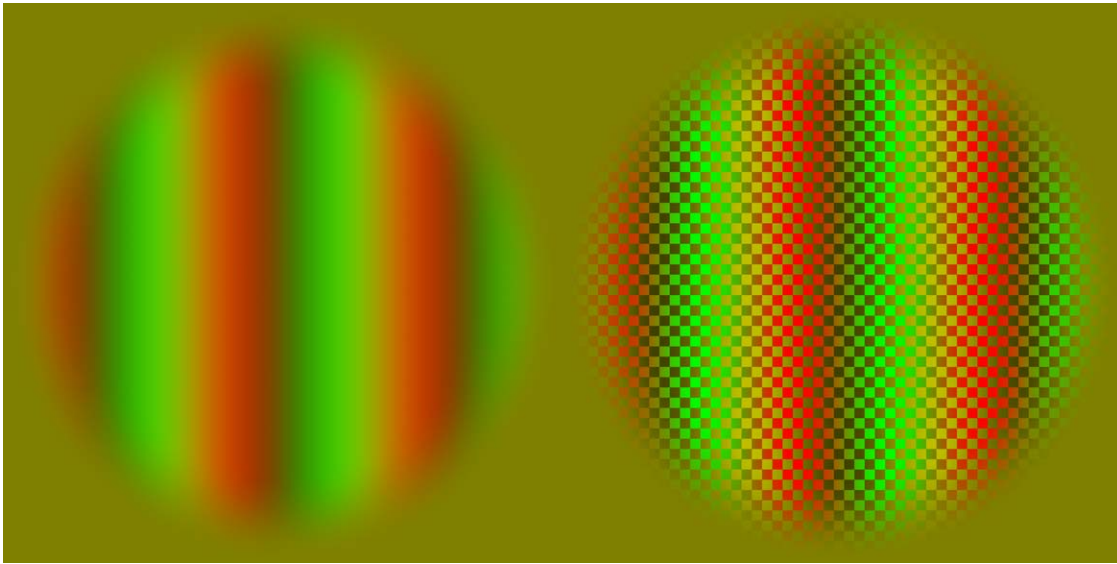
Figure 6. Superimposed luminance and color modulations that are spatially interleaved (right) or not (left).

phase interaction was due to a nonlinear response before any strong spatial integration, then this interaction should not occur when the luminance and color information are spatially interleaved. On the other hand, if the luminance-color phase interaction was due to a nonlinear response after a substantial spatial integration, then it should not matter if luminance and color information are spatially interleaved (at a high spatial frequency) since both would still be spatially integrated.

Method

The experiment was identical to the first experiment except that the luminance and color information were spatially interleaved rather than temporally interleaved. The spatial interleaving was based on a checkerboard pattern with check size of 4 × 4 pixel (i.e., 0.0625° × 0.0625°) as illustrated in Figure 6.

Results and discussion

As shown in Figure 7, a luminance-color phase interaction was observed when spatially interleaving the luminance and color information. This interaction cannot occur at the photoreceptor level where luminance and color information was processed separately. This interaction therefore suggests that there are multiplicative nonlinearities occurring after the spatial integration of the luminance and color information, that is, cells that have large receptive fields such as bipolar cells. This experiment therefore suggests the existence of nonlinearities after a substantial spatial

integration enabling some color contribution to motion and explaining some luminance-color phase interaction.

General discussion

The current study showed an interaction between luminance- and color-defined motion processing: The contribution to motion of combined luminance and color modulations varied with their phase difference. Nonlinearities *after* the merging of the L and M pathways would not predict any strong color contribution to motion in the presence of a high contrast luminance motion (Cavanagh & Anstis, 1991) and would not predict a luminance-color phase interaction. This phase interaction suggests the existence of nonlinearities *before* the merging of the L and M pathways. The phase interaction observed when spatially interleaving luminance and color information (Experiment 3) suggests that at least some interaction occurs at a level where cells have large receptive fields. The current study therefore suggests the existence of nonlinearities *after* a spatial integration stage (i.e., cells with large receptive field) and *before* the merging of the L and M pathways. Given that photoreceptors have small receptive fields and that L and M pathways merge at ganglion cells, our results are consistent with nonlinearities at the bipolar cell level.

To our knowledge, not many studies have considered late nonlinearities (i.e., after photoreceptors) enabling the luminance motion system to process color motion. Cavanagh and Anstis (1991) considered the possibility that the contrast response of luminance-sensitive
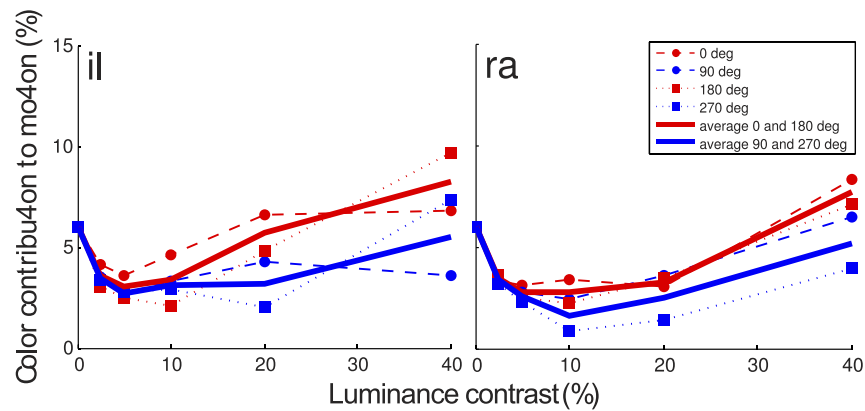
Figure 7. Color contribution to motion as a function of luminance when spatially interleaving luminance and color information. Legend as in Figure 5.

receptors was not linear as a function of the luminance contrast (e.g., proportional to $(c_L+c_M)^2$ or $(c_L+c_M)^{0.5}$, where c_L and c_M represents the contrast for L and M cones, respectively). Their simulations (see figure 20 in Cavanagh & Anstis, 1991 and dashed lines in Figure 8 below) showed that such nonlinear contrast responses could not explain the substantial color contribution to motion in the presence of a high contrast luminance-defined modulation, as the color contribution to motion would still converge to zero when increasing the luminance contrast. The rationale of Cavanagh and Anstis was to consider a nonlinear response of the luminance system. By doing so, however, they only considered nonlinearities *after* the summation of the L and M pathways, e.g., $(c_L+c_M)^2$. Expansive contrast responses *before* the summation of the L and M pathways, e.g., $c_L^2+c_M^2$, could generate a strong color contribution to motion (Figure 8) and a strong phase interaction (Figure 9). This shows that cone-specific nonlinearities can explain both the substantial color contribution to motion in the presence of high contrast luminance modulation and the phase interaction within the luminance pathway. Consequently, the substantial color contribution to motion in the presence of a high contrast luminance modulation does *not* necessarily imply the existence of a dedicated color motion system.

The positive color contribution to motion in the presence of a luminance modulation suggests that the cone-specific nonlinearity is expansive. If the contrast response function was linear, the color contribution to motion in the presence of a luminance modulation would be near zero (Figure 8, black line), with an expansive response (e.g., $c_L^2+c_M^2$) it would be positive (Figure 8, solid, blue line) and with a compressive response (e.g., $c_L^{0.5}+c_M^{0.5}$) it would be negative (Figure 8, solid, red line), which would mean that the contribution to motion of a luminance-defined modulation would be reduced by adding a color-defined modulation. Thus, the substantial positive color

contribution to motion in the presence of a high contrast luminance modulation and its dependency on the luminance-color phase difference suggests the existence of a cone-specific contrast response that is expansive, not compressive.

The current study showed that a substantial color contribution to motion in the presence of a high contrast luminance modulation could be explained by an expansive, cone-specific nonlinearity. However, such a nonlinearity cannot explain by itself the color contribution to motion at equiluminance. If there were no interunit variability in equiluminance, then applying the same expansive nonlinearity to L and M
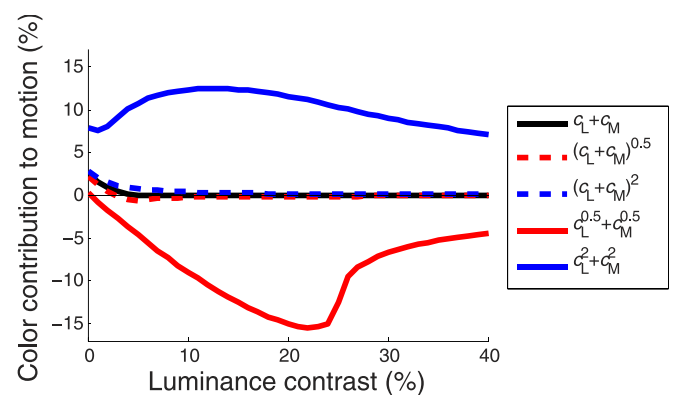

Figure 8. Simulations of the color contribution to motion as a function of luminance contrast given both interunit variability in equiluminance and nonlinearities that are either expansive (blue lines) or compressive (red lines) and occur either before (solid lines) or after (dash lines) the summation of the L and M pathways. Simulation of the color contribution to motion given interunit variability in equiluminance without any nonlinearity is represented by the black solid line. Note that for the simulations, the cone contrast of the color modulation was estimated to be 25% of the color modulation expressed in luminance contrast of red and green color guns.
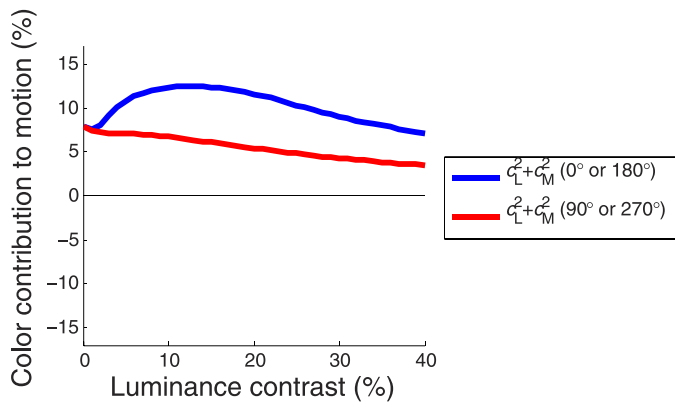
Figure 9. Simulation of the color contribution to motion as a function of luminance contrast for different luminance-color phase differences given both interunit equiluminance variance and an expansive nonlinearity before the summation of the L and M pathways. Note that for the simulations, the cone contrast of the color modulation was estimated to be 25% of the color modulation expressed in luminance contrast of red and green color guns.

pathways when a color-defined modulation is presented at equiluminance would not generate any color contribution to motion, as the sum of the L and M information would still cancel one another. However, the color contribution to motion that is not at equiluminance would be increased by an expansive, cone-specific nonlinearity (Figure 8). Thus, given some interunit variance in equiluminance point, an expansive, cone-specific nonlinearity could increase the color contribution to motion at "equiluminance." The current findings suggest that under some conditions, the color contribution to motion could be explained by the combination of interunit variability in equiluminance and an expansive, cone-specific nonlinearity.

Although many types of nonlinearities have been considered as potential luminance artifacts enabling the luminance pathway to process color-defined motion, none, to our knowledge, are compatible with both the luminance-color phase interaction observed in the present study (greater color contribution to motion luminance and color modulations are aligned, i.e., 0° and 180° phase difference, than when offset by ±90°) and the increasing color contribution to motion with luminance contrast. Thus, the current findings suggest the existence of some nonlinearity that has not been considered before, enabling some color-defined motion processing: an expansive, cone-specific nonlinearity.

Keywords: motion, color, luminance artifact, expansive nonlinearity, interunit variability in equiluminance

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