

# The contribution of color to global motion processing

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This study investigates the contribution of color vision to global motion. We present evidence demonstrating that performance on a global motion task attains similar levels for both types of chromatic (L/M-cone opponent and S-cone opponent) and luminance stimuli at suprathreshold contrasts. We show, however, that the motion thresholds for isoluminant chromatic stimuli are luminance based, on the grounds that they are masked by luminance noise but robust to chromatic noise. Detection thresholds, on the other hand, are chromatic in origin (masked by chromatic but not luminance noise), indicating that there is no luminance artifact in the stimulus. We suggest that for color vision at isoluminance the global motion task is based on the integration of many local, luminance-based signals.

**Keywords:** color vision, motion-2D, detection/discrimination

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## Introduction

The evidence for whether it is possible for human color vision to integrate chromatic global motion in isoluminant stimuli is conflicting. While one study has concluded that there is virtually no red-green input into global motion processing (Bilodeau & Faubert, 1999), another found a significant red-green input, but a non-existent S-cone input (Ruppertsberg, Wuerger, & Bertamini, 2003). This latter conclusion was revised in a subsequent study in which it was demonstrated that global motion integration is possible for stimuli that selectively isolate S-cones, but that this has a strong dependence on the choice of stimulus parameters (Ruppertsberg, Wuerger, & Bertamini, 2007). Thus, although there is evidence that color can be used in non-isoluminant global motion stimuli to enhance the motion response by acting as a cue for signal dot segregation (Croner & Albright, 1999; Edwards & Badcock, 1996; Snowden & Edmunds, 1999), the direct contribution of color contrast to global motion is unresolved.

Global motion stimuli, by definition, require the visual system to integrate the combined motion of a collection of elements and are thought to involve area MT in primates and humans (Huk & Heeger, 2002; Movshon, Adelson, Gizzi, & Newsome, 1985; Newsome, Britten, & Movshon, 1989; Newsome & Paré, 1988; Salzman, Murasugi, Britten, & Newsome, 1992). Random dot kinematograms (RDK) are one example of global motion stimuli, where each element in the RDK display is a local motion source. Since the observer finds the direction of global motion of the RDK by integrating local motion

vectors, the role of color vision in global motion depends critically on its performance in processing local motion. It has been shown (Nakayama & Tyler, 1981) that the movement of random dot patterns is detected by motion sensitive and not position sensitive mechanisms, making them ideal for studying mechanisms underlying motion discrimination. The contribution of color and luminance mechanisms to non-global motion processing, in which all local motion vectors have the same direction and there is no integration stage, has been extensively investigated. One of the key findings has been that first order (linear) motion thresholds for isoluminant stimuli can be masked by dynamic luminance noise and contain significant luminance components (Baker, Boulton, & Mullen, 1998; Lu, Lesmes, & Sperling, 1999; Lu & Sperling, 1996, 2001; Michna, Yoshizawa, & Mullen, 2007; Mullen, Yoshizawa, & Baker, 2003; Yoshizawa, Mullen, & Baker, 2000). In comparison, detection thresholds for isoluminant stimuli are not masked by luminance noise but are masked by chromatic noise, indicating that they are chromatic in origin. The selectivity of luminance noise masking for chromatic motion thresholds but not detection thresholds for isoluminant stimuli suggests a biological rather than a stimulus origin of an induced luminance response to a moving chromatic stimulus.

The aims of this study are twofold. First, we compare performance on global motion discrimination for chromatic and luminance stimuli; we vary both the contrast and the coherence level of the stimuli as some of the discrepancies in the results of previous studies may arise because the effects of stimulus contrast and motion coherence interact. Second, we address for the first time the nature of motion discrimination for isoluminant

chromatic global motion stimuli by using dynamic luminance and chromatic noise to mask the stimulus motion in order to determine whether the chromatic global motion task is based on chromatic or luminance responses.

The stimuli were random dot kinematograms (RDKs) (Braddick, 1980; Newsome & Paré, 1988; Ramachandran & Gregory, 1978) and are displays of moving Gaussian blobs with a specified motion coherence (defined as the percentage of the Gaussian blobs that are moving in a common direction), and observers must indicate the direction of their motion. The stimuli were designed to either isolate the L/M (red-green) or S (blue-yellow) cone opponent or the luminance mechanism. We used a limited lifetime paradigm, in which Gaussian blobs appear for a designated time and are then repositioned, which minimizes the ability of the observer to track any individual blob.

## Methods

### Apparatus

Stimuli were presented on a PC-controlled Cambridge Research Systems (CRS) ViSaGe stimulus generator, connected to a 21-inch. SONY GDMF500 CRT-monitor. Stimulus presentation was synchronized with the screen refresh rate of 120 Hz. The ViSaGe specifies colors with a resolution of 14 bits per CRT gun. The spatial resolution of the screen was  $1104 \times 828$  pixels. The luminance output of the CRT guns is non-linear and this was corrected with look-up tables using the ViSaGe calibration system (OptiCAL, Cambridge Research Systems). The chromaticities of the red, green, and blue phosphors were measured using a Photo Research PR-700 PC Spectrascan. The stimuli were viewed monocularly in a darkened room and responses were collected using a Cambridge Research Systems CT3 button box.

### Observers

Five observers participated in these trials, four naive to the purposes of the experiment (CAS, DG and JT) and two authors (MM and KTM). All had normal to corrected-to-normal visual acuity and normal color vision as assessed using the Farnsworth-Munsell 100-Hue test.

### Stimuli

The limited lifetime RDKs were generated using MatLab, where motion sequences were generated with 50 chromatic or luminance Gaussian blobs (with  $\sigma = 0.25^\circ$  and an FWHM of  $0.58^\circ$ ). The stimulus (diameter of  $12^\circ$

visual angle) was presented on a gray background with a luminance of  $50 \text{ cd/m}^2$ . The Gaussian blobs appeared and disappeared with a life time duration of 240 ms, starting at different temporal phases on a frame by frame basis (i.e., the number of blobs that appear or disappear at each frame is statistically the same). All blobs had the same speed of  $5.4 \text{ deg/s}$ . Overall stimulus presentation was ramped on and off in a Gaussian temporal envelope ( $\sigma = 0.125 \text{ s}$ ). For the first experiment only (Figure 1), stimulus contrast was threshold scaled (i.e., presented in multiples of detection threshold), and for these detection threshold measurements, a black occluder of  $6^\circ$  diameter was placed over the center of the stimulus field.

### Color space

The stimuli were designed to isolate the L/M (red-green, RG) and S (blue-yellow, BY) cone opponent mechanisms and the luminance mechanism. Stimuli were represented within a three-dimensional cone contrast space (Cole, Hine, & McIlhagga, 1993; Noorlander & Koenderink, 1983; Sankeralli & Mullen, 1996; Stromeyer, Cole, & Kronauer, 1985), whose L-, M-, and S-cone axes were scaled in contrast units and so were independent of the mean luminance and chromaticity of the background. Stimulus contrast is defined as the vector length (root mean square) in the cone contrast space. The three cardinal stimuli were used. A cardinal direction under the definition by Cole et al. (1993) represents the stimulus direction that isolates one postreceptoral detection mechanism from the other two. The achromatic (ACH) stimulus vector lies in the equally weighted +L, +M, +S direction (white isochromatic) of the (L, M, S) cone contrast space and represents the luminance cardinal direction. S-cone stimuli (BY) were modulated along the +S (blue) direction of the S-cone axis, which is the cardinal direction of the S-cone opponent mechanism. We verified that our stimuli were effectively isolating the S-cones for each subject by using a perceptual task. A Gabor stimulus (with spatial frequency of  $0.5 \text{ cpd}$ ) of fixed cone contrast was used and its vector direction in cone contrast space within the isoluminant plane was varied by the subject using a method of adjustment to find a minimum in perceived visibility. Maximum visibility occurs for the stimulus direction that lies closest to the direction of the L/M isoluminant cone opponent axis, and minimum visibility occurs when only the S-cone mechanism is activated and the L/M-cone opponent mechanism is silenced. For all our subjects, the point of minimum visibility corresponded to the vector direction of the S-cone axis, confirming that this is the cardinal direction of the S-cone opponent mechanism.

The cardinal L/M-cone opponent stimuli (RG) were in the +L-M (isoluminant red) vector direction for each subject. We determined the point of isoluminance for each observer using a minimum motion technique, in which

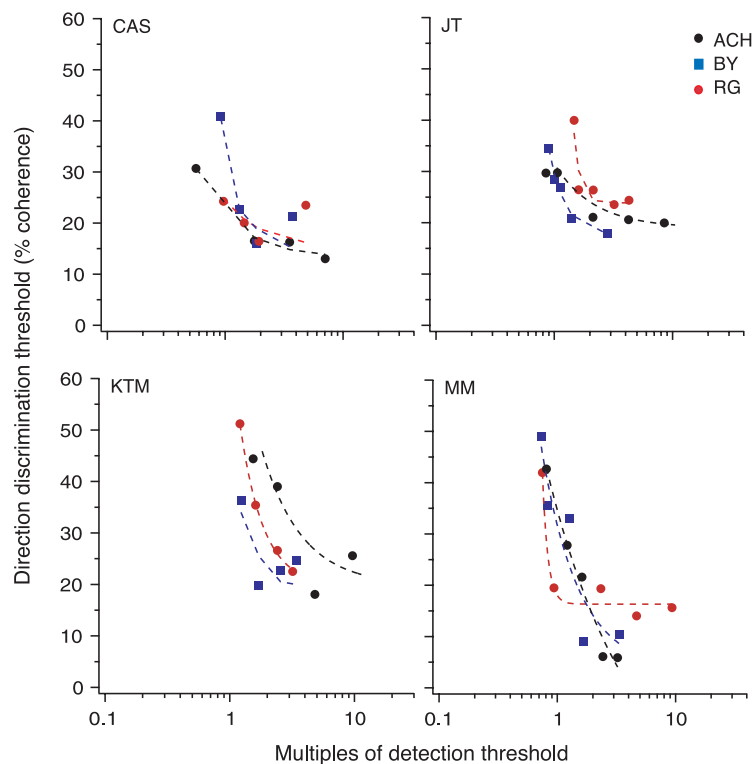


Figure 1. Thresholds for discrimination of motion direction measured as percent coherence (proportion of Gaussian blobs moving in a common direction) plotted as a function of contrast scaled in units of detection threshold for chromatic red (L/M-cone, RG), blue (S-cone, BY), and white (luminance, ACH) cardinal stimuli. The detection thresholds used for the contrast scaling were measured using an annular version of the global motion stimulus as described in the text. (Note that the motion discrimination thresholds were measured using the full stimulus). Dashed lines show a power function fit to the data (see legend of Table 1). Motion discrimination asymptotes to near-constant values at supra-threshold contrast, and performance averaged across subjects is similar for all three stimuli (see Table 1 for results of the fit). The contrast detection thresholds used for threshold scaling were CAS: ACH = 0.035, BY = 0.068, RG = 0.005; JT: ACH = 0.029, BY = 0.089, RG = 0.005; KTM: ACH = 0.025, BY = 0.059, RG = 0.004; MM: ACH = 0.027, BY = 0.075, RG = 0.006.

observers adjusted the direction of the chromatic stimulus vector (i.e., ratio of L- to M-cone contrasts) within the L/M plane to find a perceived minimum motion of a single Gabor with a stationary envelope and a continuously drifting (3 Hz) 1 cpd carrier. Averages of 30 such measurements were acquired, using monocularly and binocularly determined values. The isoluminant points (ratio of M-cone weight relative to the L) used for each subject were: CAS =  $-12.43$ , DG =  $-4.58$ , KTM =  $-3.52$ , JT =  $-5.71$ , MM =  $-7.92$ .

## Psychophysical procedure

In the detection task, a two-alternative forced-choice staircase procedure (2AFC) was used with presentation intervals of 1 s each separated by 500 ms. The subject indicated in which interval the test stimulus appeared (the other was blank). A small black fixation point was displayed before and after stimulus presentation at the center of the screen. Audio feedback was provided. A reversal was defined when the subject responded incorrectly after a minimum of two consecutive correct

responses. Each staircase terminated after six reversals. The first reversal was used to establish the threshold level, and after the first reversal, stimulus contrast was raised by 25% following one incorrect response and lowered by 12.5% following two consecutive correct responses. For a given 2AFC staircase session, the number of total trials fluctuated between 30 and 60 trials. This number guarantees a reliable threshold estimation according to the number of reversals designed (Rammsayer, 1992). The threshold value was calculated as the arithmetic mean of the last five reversals of the staircase at the 81.6% correct detection level (Mullen & Sankeralli, 1999; Sankeralli & Mullen, 1996, 1997; Sankeralli et al., 2002). Each plotted threshold is based on the average of a minimum of four staircase measurements.

In the motion discrimination task, we used the method of constant stimuli (MCS) to acquire thresholds, in which a single interval was used within the same temporal envelope as the staircase procedure. The subject indicated in which of two directions (left or right) the stimulus moved. A minimum of 40 trials for motion discrimination were performed for each condition, and psychometric functions were fitted to the data using a Weibull

distribution function (Weibull, 1951) with thresholds evaluated at the 81% accuracy level.

## Luminance and chromatic noise

We superimpose luminance (AC) noise on our test stimuli to mask luminance mechanisms and chromatic noise to mask chromatic mechanisms and measure thresholds for both detection and direction discrimination to determine whether the mechanisms for stimulus detection and motion discrimination were luminance or color sensitive. The noise was presented for 50 ms before and after each stimulus presentation. Both the luminance and chromatic noise masks were spatially two-dimensional, temporally dynamic, and this spatio-temporally flat noise was filtered with a spatially low-pass filter (Butterworth digital filter, as detailed in Yoshizawa et al., 2000) to reduce possible luminance artifacts from chromatic aberrations in the case of color noise (Bradley, Zhang, & Thibos, 1992). This filter had a cut-off frequency of 3 cpd and reduced amplitude by 40 dB at 4 cpd. The noise contrast was defined by RMS contrast  $C_{\text{rms}} = C / \sqrt{3}$  in cone contrast units and the maximum cone contrast available was 28.9%, taking into account the frame interleaving of the test stimulus and noise mask. We note that the contrast is also limited by the gamut of the color space, depending on the vector direction (color) of the stimulus used.

## Results

In the first experiment, we measured motion discrimination as a function of stimulus contrast. Figure 1 plots motion discrimination thresholds for white (luminance), red (L/M-cone isolating), and blue (S-cone isolating) Gaussian blobs as a function of the cone contrast (scaled in multiples of detection threshold). We have expressed stimulus contrast in threshold-scaled units (multiples of detection threshold) in order to control for the effects of stimulus visibility on motion coherence thresholds. However, rather than using fovea detection thresholds to scale the stimuli, we have used thresholds based on the more peripheral stimulus regions for the following reasons. It has been demonstrated that in human vision, chromatic and luminance contrast sensitivity have a differential distribution across the visual field, and in particular there is a steeper loss of RG chromatic (L/M-cone opponent) contrast sensitivity than luminance (Mullen, 1991; Mullen & Kingdom, 2002). Hence, regular detection thresholds obtained for 12° stimuli reflect sensitivity of the fovea, and the differential sensitivity to the three cardinal stimuli at the fovea, and when presented at low multiples of detection threshold, only a small central part of the

stimulus will be visible. Since the visual system integrates global motion across the entire stimulus, and not just at the fovea, we measured detection thresholds for the more peripheral regions of the stimulus by placing a circular black occluder (diameter = 6°) in front of the motion stimulus (diameter = 12°) to eliminate the contribution of central vision to contrast detection thresholds. Therefore, our contrast scaling is more appropriate for the global motion task since it includes the least visible, more peripheral regions of the stimulus and ensures that both foveal and peripheral regions of the three types of stimuli will be visible to the observer even when presented at low multiples of detection threshold. Moreover, the relative contrast scaling between the three cardinal stimuli also takes into account the more peripheral rather than the central regions. This has the effect in Figure 1 of bringing the performance curves for each color closer together horizontally than if foveal values were used.

It is evident in Figure 1 that thresholds for discriminating global motion follow a similar pattern for all three stimulus types, with the highest coherence thresholds obtained at the lowest contrasts near detection threshold. As the contrast of the stimuli increases, the coherence thresholds decrease and tend to asymptote to a stable level that is contrast independent, a pattern that has been demonstrated in previous results for luminance stimuli (Edwards, Badcock, & Nishida, 1996; Simmers, Ledgeway, & Hess, 2005). The asymptotic coherence thresholds for each observer for all three stimuli types are presented in Table 1, in which it can be seen that all three performances averaged across subjects asymptote to similar values. The average across all observers was

	Luminance Gaussian blobs	Red Gaussian blobs (L/M-cone opponent)	Blue Gaussian blobs (S-cone isolating)
CAS	13.26	16.17	19.67
JT	18.97	23.87	17.29
KTM	21.55	19.63	20.58
MM	9.16	20.24	13.21
Average (± standard deviation)	15.74 ± 5.59	19.98 ± 3.15	17.68 ± 3.29

Table 1. Thresholds (% coherence) for discrimination of motion direction for chromatic red (L/M-cone), blue (S-cone), and white (luminance) stimuli. The relationship between the threshold for global motion discrimination and the magnitude of the dot contrast can be described by a power function plus a constant  $y = a * x^b + c$ , where  $a$ ,  $b$ , and  $c$  are parameters. Fitting this power function to the data in Figure 1, we extract the % coherence value at which the curves asymptote, corresponding to the constant  $c$  in the power relation. These values are given in this table, where the average across all observers was  $17.8 \pm 4.2\%$ .



$17.8 \pm 4.2\%$ . The results for subject MM, although slightly different from the other observers, were repeatable.

## Luminance noise masking

The effects of luminance noise on threshold, as previously outlined, are effective in revealing whether the neural mechanisms for stimulus detection or discrimination are sensitive to luminance contrast. Figure 2 shows

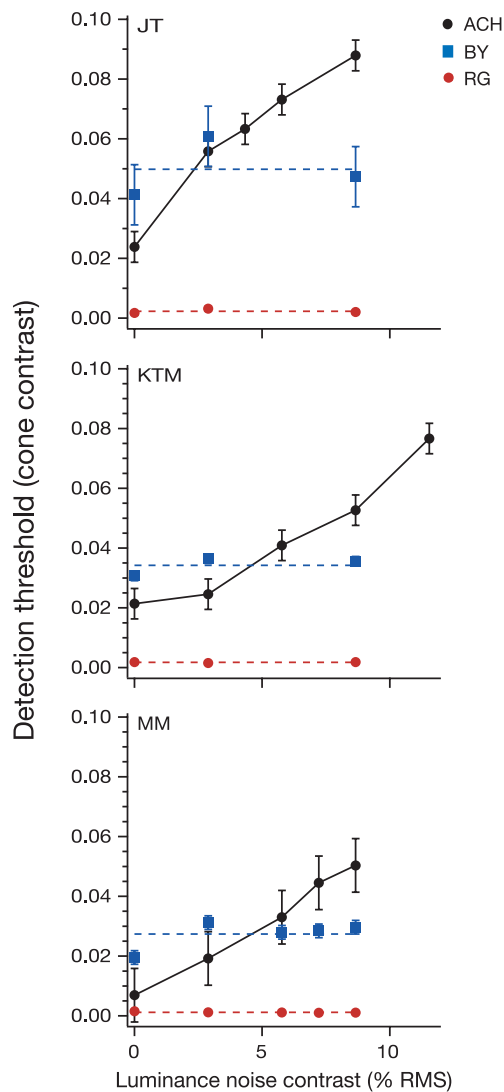


Figure 2. Contrast detection thresholds for global motion stimuli, as described in Figure 1, plotted as a function of the contrast of a dynamic two-dimensional luminance noise mask. The noise contrast was defined by RMS contrast in cone contrast units. Contrast detection thresholds for luminance stimuli rise with increasing luminance noise contrast, but those for chromatic stimuli are unaffected by the noise mask. Dashed lines indicate a horizontal fit to data points. Note that all thresholds are for the full RDK stimulus. Error bars show  $\pm 1$  SD and may be smaller than the symbol size.

contrast detection thresholds for the luminance and chromatic RDKs as a function of increasing two-dimensional luminance noise contrast. It can be seen that for blue (S-cone isolating) and red (L/M-cone isolating) stimuli, thresholds for stimulus detection are unaffected by increasing luminance noise contrast, whereas thresholds for stimulus detection of the white (luminance) RDKs increase with increasing luminance noise contrast.

This demonstrates that the detection of the cardinal chromatic stimuli is independent of luminance noise and is therefore mediated by chromatic mechanisms, as expected from previous results (Gegenfurtner & Kipper, 1992; Losada & Mullen, 1994; Sankeralli & Mullen, 1997). The results also validate the effectiveness of luminance (AC) noise for masking luminance Gaussian stimuli.

Thresholds for discrimination of motion direction as a function of increasing luminance noise contrast are shown in Figure 3 for all three stimulus types. The contrast values of the test stimulus for each subject and each stimulus type were chosen to be high enough for motion discrimination to be contrast independent (i.e., on the asymptote of the coherence threshold vs. contrast function), based on the data of Figure 1. It can be seen that motion discrimination thresholds rise as a function of increasing luminance noise contrast for all three stimulus types, indicating that mechanisms sensitive to luminance contrast are mediating motion thresholds for both isoluminant chromatic and luminance global motion RDKs. This differs from the results for detection thresholds (Figure 2) in which luminance noise only masks the detection of luminance stimuli. Hence, for the two chromatic stimuli, the luminance noise masks motion discrimination thresholds but not detection thresholds, and the gap between detection and motion discrimination thresholds increasingly widens with noise contrast. Thus, at high noise contrasts the stimulus visibility is unchanged but the motion disappears, leaving the RDK stimulus static in appearance. It has been demonstrated previously, using different types of local motion, that motion thresholds for isoluminant stimuli may be susceptible to luminance noise masking; specifically in the case of linear motion, direction discrimination appears to be performed via luminance mechanisms for both types of isoluminant chromatic stimuli (Baker et al., 1998; Michna et al., 2007; Mullen et al., 2003; Yoshizawa et al., 2000).

The masking effects were fitted using a generalization of Burgess, Wagner, Jennings, and Barlow (1981) and Pelli (1990) noise-masking functions, which relates the power (contrast squared) of the test stimulus at threshold ( $P_t$ ) to the internal noise power ( $P_i$ ), the external noise ( $P_e$ ) as well as the sampling efficiency ( $\eta$ ) (Mullen et al., 2003):

$$P_t = P_i + P_e/\eta. \quad (1)$$

The internal noise ( $P_i$ ) affects thresholds when no external noise is present in the stimulus, referred to as the

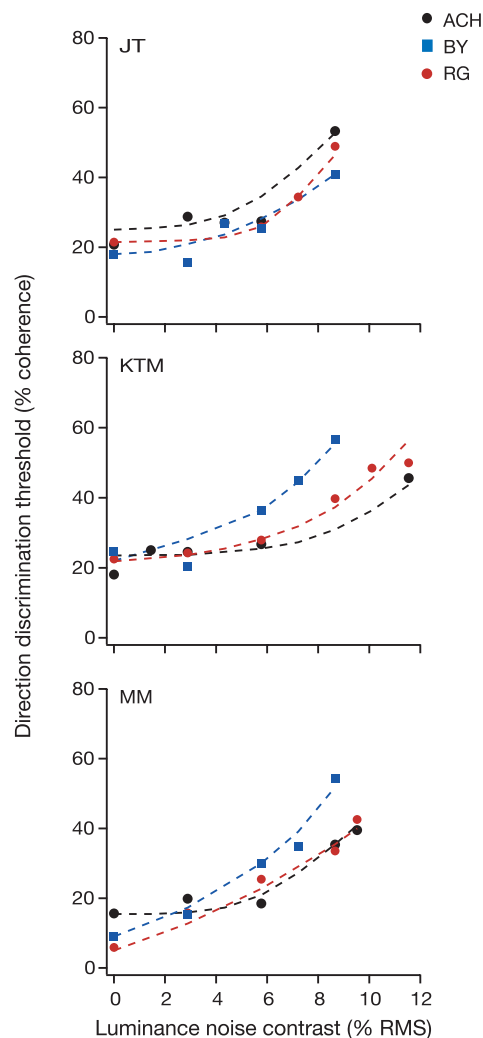


Figure 3. Thresholds for direction discrimination (% coherence) for isoluminant red (L/M-cone isolating), blue (S-cone isolating), and white (luminance) global motion stimuli plotted as a function of the RMS contrast of a dynamic two-dimensional luminance noise mask, as used in Figure 2. Motion thresholds for all three stimulus types rise with increasing luminance noise contrast indicating a luminance response to motion discrimination. Symbols are as in Figure 1. Test stimulus contrasts were JT: ACH = 0.26, BY = 0.28, RG = 0.02; KTM: ACH = 0.25, BY = 0.32, RG = 0.035; and MM: ACH = 0.20, BY = 0.25, RG = 0.03. Dashed lines represent the model fits using Equation 1. Note that all thresholds are for the full RDK stimulus.

observer's equivalent noise and the constant  $\eta$  is proportional to the sampling efficiency. The dashed lines in Figure 3 represent the fits to the data made using Equation 1. We find no evidence for any differences between the fits for the three stimulus types.

### Red-green chromatic noise masking

The results above demonstrate that the mechanisms mediating motion discrimination for isoluminant chromatic

RDks appear to be responsive to luminance contrast. In order to confirm that these mechanisms are not chromatic, or a hybrid of luminance and chromatic mechanisms, we superimposed two-dimensional dynamic chromatic noise on our stimuli, with the intention of revealing any chromatic sensitivity of the detection and the motion responses. For example, if the mechanisms mediating motion of the L/M chromatic stimuli are color sensitive, red-green (L/M-cone isolating) noise will mask motion discrimination for red-green (L/M-cone isolating) stimuli.

The results in Figure 4 show contrast detection thresholds for luminance and both types of chromatic stimuli. It is evident that contrast detection thresholds for red (L/M-cone isolating) stimuli increase with increasing noise contrast but for white (luminance) and blue (S-cone isolating) stimuli, thresholds are relatively unattenuated

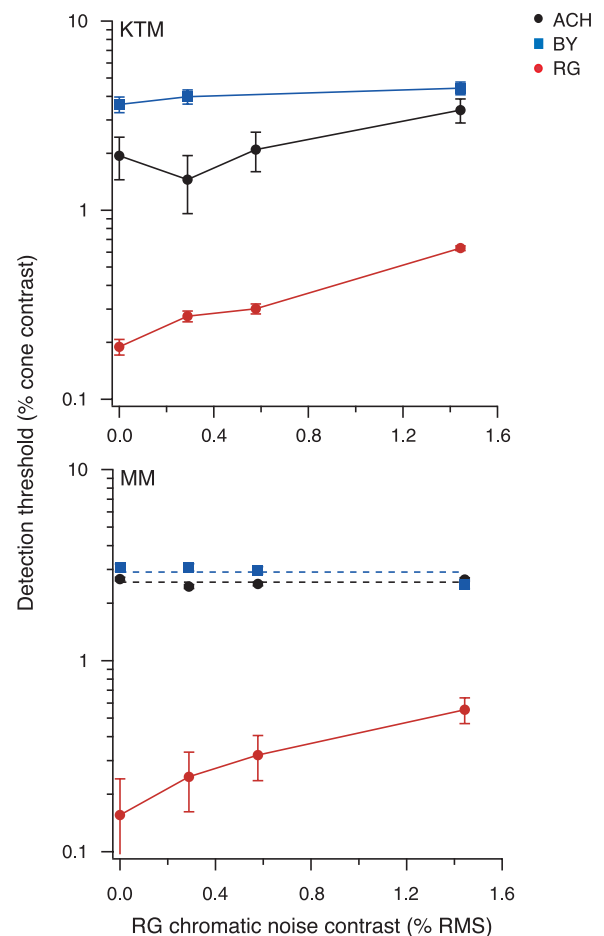


Figure 4. Contrast detection thresholds for global motion stimuli, as described in Figure 1, plotted as a function of RMS contrast for isoluminant red-green (L/M-cone isolating, RG) masking noise. Results demonstrate an increase in thresholds for red (L/M-cone isolating) stimuli and a smaller or no increase for BY and Ach test stimuli. Dashed lines indicate a horizontal fit to data points. The maximum RMS contrast available for the RG noise was 1.45%, limited by the color gamut and frame interleaving (see Methods). Error bars show  $\pm 1$  SD and may be smaller than the symbol size.

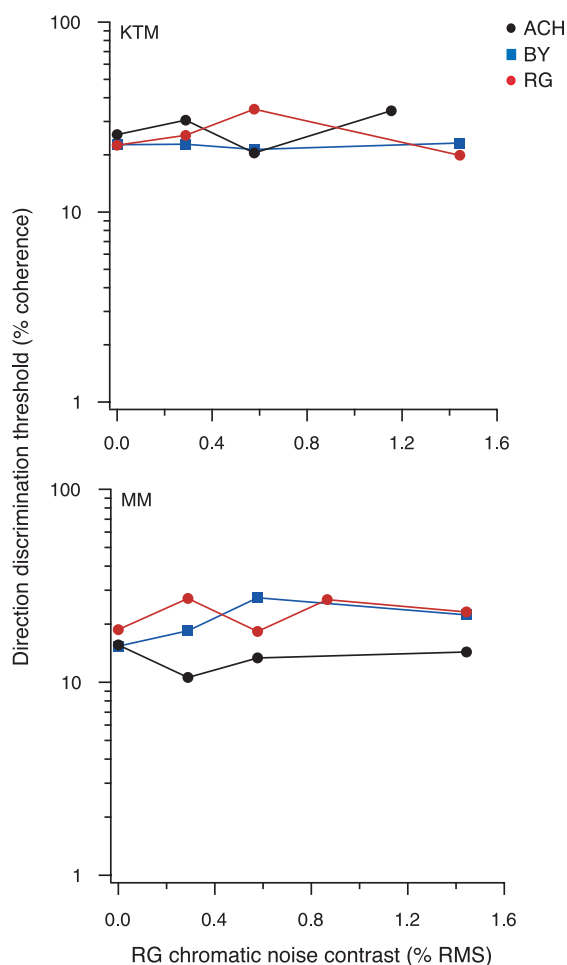


Figure 5. Thresholds for direction discrimination (% coherence) for isoluminant red (L/M-cone isolating), blue (S-cone isolating), and white (luminance) global motion stimuli plotted as a function of RMS contrast for isoluminant red-green (L/M-cone isolating, RG) masking noise, as used in Figure 4. Thresholds for all three stimulus types remain stable as a function of increasing RG noise contrast, indicating a chromatic response does not mediate motion discrimination. Symbols are as in Figure 1.

with increasing red-green chromatic noise contrast. This is as expected if detection of the L/M-cone opponent stimuli is mediated via an L/M-cone opponent chromatic system, and detection for the luminance stimuli is mediated via luminance mechanisms. The detection of blue (S-cone) stimuli is also relatively unattenuated with increasing contrast noise, indicating that detection of the L/M-cone opponent global motion elements is mediated via a chromatic mechanism separable from the blue-yellow mechanism. Results showing reduced or absent cross masking of detection thresholds for cardinal test stimuli by RG chromatic noise have been reported previously for grating stimuli (Gegenfurtner & Kipper, 1992; Giulianini & Eskew, 1998; Losada & Mullen, 1995; Sankeralli & Mullen, 1997).

In the case of direction discrimination (Figure 5), coherence thresholds for all three stimuli are relatively constant with increasing L/M chromatic noise contrast,

demonstrating that motion discrimination for L/M-cone isolating chromatic stimuli is not performed via chromatic mechanisms and, based on the results in Figure 3, that luminance mechanisms are active in motion discrimination. The motion response is thus luminance based and not a hybrid of chromatic and luminance mechanisms. These motion results are similar to those of some previous studies with different local motion stimuli, which show a luminance-based system for motion processing of linear chromatic motion (Baker et al., 1998; Mullen et al., 2003; Yoshizawa et al., 2000; Yoshizawa, Mullen, & Baker, 2003).

## Blue-yellow chromatic noise masking

In the case of masking using dynamic blue-yellow (S-cone isolating) noise, we would expect based on results

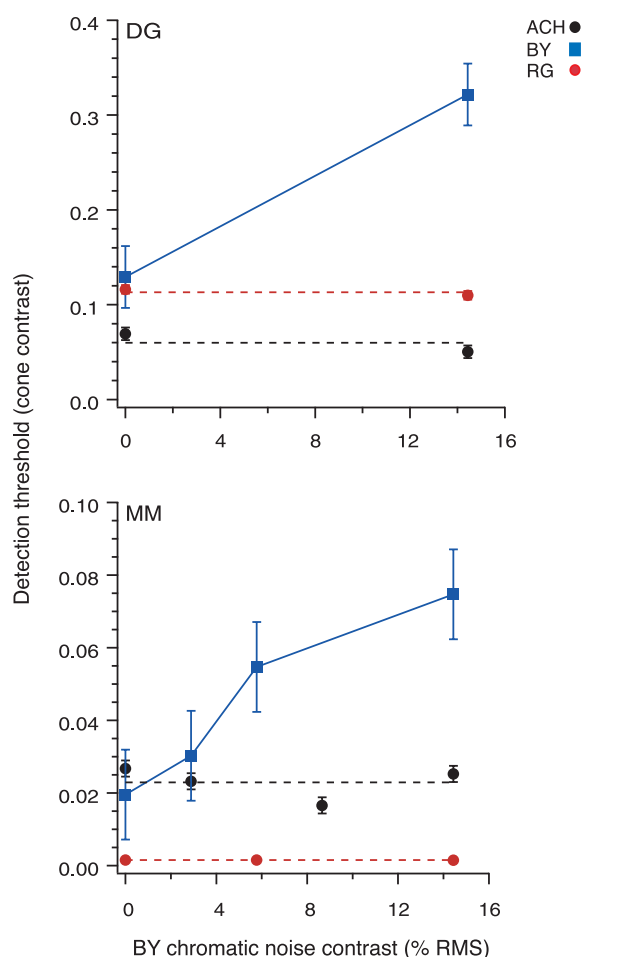


Figure 6. Contrast detection thresholds for global motion stimuli, as described in Figure 1, plotted as a function of RMS contrast for isoluminant blue-yellow (S-cone isolating, BY) masking noise. Results demonstrate an increase in thresholds for blue (S-cone isolating) stimuli only. Dashed lines indicate a horizontal fit to data points. Error bars show  $\pm 1$  SD and may be smaller than the symbol size.

using other stimulus types that contrast detection thresholds for blue (S-cone isolating) stimuli would be masked as a function of increasing noise contrast (Michna et al., 2007; Sankeralli & Mullen, 1997). Figure 6 demonstrates that thresholds for detection of blue (S-cone isolating) stimuli increase with increasing noise contrast, demonstrating the effectiveness of the S-cone isolating noise as a mask for these stimuli, whereas thresholds for luminance and red (L/M-cone isolating) stimuli are relatively unattenuated.

In the case of motion discrimination, we demonstrate in Figure 7 that direction discrimination thresholds for all three stimuli are unaffected by increasing blue-yellow (S-cone) chromatic noise contrast. Therefore, these results in combination with the results of Figure 3, in which

motion discrimination thresholds for S-cone stimuli are masked by luminance noise, suggest that motion discrimination for S-cone isolating chromatic stimuli is performed via luminance and not chromatic mechanisms. This is consistent with previous findings for two-flash linear motion using S-cone isolating stimuli (Michna et al., 2007).

## Discussion

Although the issue as to whether the human visual system can perceive motion from purely chromatic moving stimuli has been widely investigated, the case for chromatic global motion has received much less attention. Our results are novel in that we have demonstrated that the chromatic and luminance systems perform equally well in integrating global motion at suprathreshold contrasts: performance becomes independent of contrast at suprathreshold contrasts, with both of the color mechanisms and the luminance mechanism reaching similar performance levels. Some previous studies that have addressed the role of the chromatic system in global motion discrimination have found that there is some form of global motion processing available to the chromatic system for RDKs (Edwards & Badcock, 1996; Ruppertsberg et al., 2007; Snowden & Edmunds, 1999). In contrast, the work of Bilodeau and Faubert (1999) found that the chromatic system was extremely poor at integrating global motion signals. This latter study compared threshold coherence for both isochromatic and RG isoluminant RDK global motion stimuli (using 15% equivalent cone contrast) and concluded that the chromatic and the luminance systems have independent motion analyzers based on the very high motion discrimination thresholds (>50% coherence) obtained for chromatic RDKs. We have been unable to replicate such high coherence thresholds in our study. We suggest that it is possible that the high coherence thresholds reported by Bilodeau and Faubert (1999) were influenced by their use of a diffusing screen through which subjects viewed the RDKs, in an effort to soften stimulus edges. We repeated some of our threshold measurements on MM and KTM using our RDK stimuli (with no masking noise) under the conditions used in Figure 1 but placing a diffusing screen made from three sheets of tracing paper in front of our isoluminant or isochromatic RDK stimuli. We found that thresholds for motion discrimination increase significantly (by at least a factor of two) based on decreased stimulus visibility and the coalescing of the enlarged stimulus dots. Thus, the use of a diffuser may at least partially explain why the RG coherence thresholds presented by Bilodeau and Faubert (1999) are higher than ours.

In contrast, another study reported some global motion processing for the red-green cone opponent chromatic

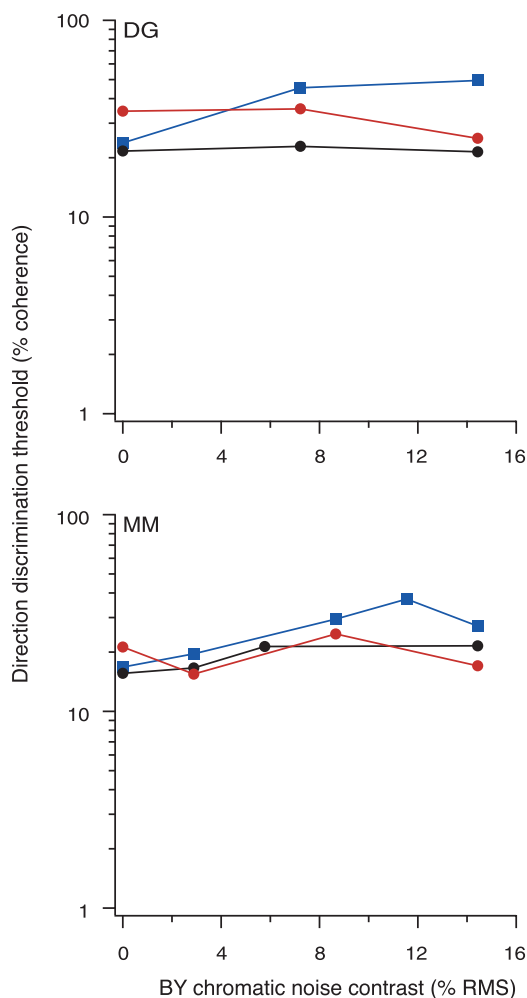


Figure 7. Thresholds for direction discrimination (% coherence) for isoluminant red (L/M-cone isolating), blue (S-cone isolating), and white (luminance) global motion stimuli plotted as a function of RMS contrast for blue-yellow (S-cone isolating) masking noise. Thresholds for all three stimuli types remain stable as a function of increasing chromatic noise contrast, indicating a chromatic response does not mediate motion discrimination. Symbols are as in Figure 1.



system, but failed to find any for the blue-yellow cone opponent system (Ruppertsberg et al., 2003). In a subsequent study, these authors (Ruppertsberg et al., 2007) increased stimulus size and used S-cone isolating isoluminant RDK stimuli to compare color contrast thresholds for detection and motion discrimination at a fixed motion coherence level (40%). They found that stimulus size and displacement were the deciding factor for whether global motion integration was possible for S-cone isolating stimuli. Both of these studies implied a relatively poor performance of chromatic global motion based on a large gap between contrast thresholds for detection and motion discrimination, although no specific comparisons are made with luminance stimuli. This differs from our finding that all three stimulus types show similar response curves when measured as a function of contrast (scaled in units of detection threshold) and asymptote to similar levels of performance in the absence of luminance noise. The size of the gap found by Ruppertsberg et al. (2003, 2007) between detection and motion thresholds is the basis for their conclusion that color is a poorer at global motion than luminance vision. The size of this gap, however, is variable and depends on the stimulus parameters chosen. First, it will depend on the coherence level selected for the stimuli; as examination of Figure 1 shows, high motion coherences favor motion discrimination down to lower contrasts, whereas low motion coherences require higher contrasts to be discriminated. Second it is particularly large in the Ruppertsberg et al. studies because their detection thresholds are foveal thresholds and so will be very low, whereas global motion contrast thresholds depend on the integration of the full stimulus field, requiring the perifoveal stimulus regions, and so are necessarily higher. We compensated for this foveal-peripheral confound by eliminating the central part of the stimulus when contrast scaling our stimuli in multiples of detection threshold and found that performance as a function of contrast was similar for both chromatic (RG and BY) and the luminance stimuli (Figure 1). In control experiments, we measured detection thresholds for stimuli that included the central region, and we found that the consequent lowering of the detection threshold increases the detection/motion discrimination threshold gap to levels approximating those of Ruppertsberg et al. (2007). Thus, it is important to explore fully the interactions between stimulus contrast and coherence for chromatic and luminance stimulus types, as we have done here, to establish a more complete picture of the relationship between chromatic and luminance performance.

Our results are also novel because they address the nature of the mechanisms mediating global motion discrimination. Specifically, although we find similar motion performance for chromatic and luminance systems, we still demonstrate a failure of color vision for global motion because we show that the motion thresholds are based on a luminance and not a chromatic signal, which we argue is of biological origin. Through the use of

a noise-masking paradigm, we have demonstrated that chromatic global motion thresholds are masked by luminance and not chromatic noise, indicating a luminance but not a chromatic contribution to the global motion processing of isoluminant stimuli. The results presented here are consistent with previous studies that have analyzed motion discrimination for other (non-global) motion stimuli and found them to be luminance based, specifically when the motion mechanisms are linear in origin (Baker et al., 1998; Cavanagh & Favreau, 1985; Lee & Stromeyer, 1989; Michna et al., 2007; Mullen et al., 2003; Stromeyer, Kronauer, Ryu, Chaparro, & Eskew, 1995; Yoshizawa et al., 2000, 2003). When isoluminant chromatic motion is based on nonlinear (second order) motion mechanisms, there is evidence that responses are genuinely chromatic (Baker et al., 1998; Cropper & Derrington, 1994; Dobkins & Albright, 1993; Lu et al., 1999; Michna et al., 2007; Yoshizawa et al., 2000). Thus, our findings that luminance noise effectively masks the motion discrimination of isoluminant global motion RDKs implies that the underlying local motion mechanisms are likely to be linear as well as luminance based.

It has been suggested that global-motion extraction is a two-stage motion process, the first stage being the extraction of the local-motion vectors. For the motion extraction of the first-order spatial patterns, this involves some form of motion energy extraction (Adelson & Bergen, 1985) and is probably performed by the motion sensitive cells in V1. Motion extraction of higher-order spatial patterns involves a nonlinear step (Chubb & Sperling, 1988), which may be performed by motion sensitive cells in area V2. The second stage of global motion is an integration of these local motion signals to extract the global motion direction, a task thought to be processed in area MT, based on neurophysiological and fMRI results (Huk & Heeger, 2002; Movshon, 1990; Movshon et al., 1985; Newsome et al., 1989; Salzman et al., 1992), primate lesion studies (Newsome & Paré, 1988), and clinical studies (Baker, Hess, & Zihl, 1991; Vaina, Lemay, Bienfang, Choi, & Nakayama, 1990). Here, we conclude that global motion integration of isoluminant chromatic stimuli appears to be mediated by a biologically based luminance response and is not based on purely chromatic mechanisms, although from our data we are unable to specify whether the luminance response to the chromatic stimulus arises at the first stage (extraction of local motion) or second stage (integration) of processing. Previous literature suggests that local motion of both L/M-cone opponent and S-cone opponent isoluminant stimuli may be luminance based (Baker et al., 1998; Michna et al., 2007; Mullen et al., 2003; Yoshizawa et al., 2000, 2003), consistent with the idea that the luminance response to chromatic motion arises at a relatively early stage in visual processing. There is good evidence to support the idea that M cells respond to L/M-cone opponent stimuli even at isoluminance (Lee, Martin, & Valberg, 1989a, 1989b; Lee & Sun, 2004;

Smith, Lee, Pokorný, Martin, & Valberg, 1992; Wiesel & Hubel, 1966), and this may be the origin of the psychophysical luminance response to moving red-green chromatic stimuli that we observe. There is also evidence to support an S-cone contribution to the M cell pathway (Chatterjee & Callaway, 2002). The higher stage of motion integration in MT would presumably be applied in the same way to all M cell responses whether they originally arise from chromatic or luminance stimuli. Many studies have demonstrated a response of MT to chromatic stimuli using neurophysiological and fMRI methods (Gegenfurtner et al., 1994; Mullen, Dumoulin, McMahon, de Zubicaray, & Hess, 2007; Saito, Tanaka, Isono, Yasuda, & Mikami, 1989; Seidemann, Poirson, Wandell, & Newsome, 1999; Thiele, Dobkins, & Albright, 2001; Wandell et al., 1999), although these do not generally determine whether the MT response is chromatic or luminance in nature, leaving open the question of whether there is a genuine chromatic responses to motion in area MT. It has been shown that S-cones contribute to primate MT neurons through both cone additive and, to a lesser extent, cone opponent responses (Barberini, Cohen, Wandell, & Newsome, 2005), with the cone additive response potentially providing a basis for our psychophysical result demonstrating an S-cone input to MT that is processed as a luminance-based response.

## Conclusions

We have used limited lifetime RDKs to investigate the role of the chromatic system in global motion processing. We have found that motion discrimination thresholds for isoluminant chromatic RDKs are masked by two-dimensional dynamic luminance noise, but not chromatic noise, and hence we conclude that motion processing for chromatic RDKs is based on a luminance response, probably arising at the stage of local, linear motion of the elements rather than the integration of global motion. In contrast, detection thresholds for the same stimuli are processed via chromatic mechanisms, supporting the idea that the luminance signals are biologically and not stimulus based.

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