



Luminance mechanisms mediate the motion of red–green isoluminant gratings: the role of “temporal chromatic aberration”

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Abstract

In this paper we use a dynamic noise-masking paradigm to explore the nature of the mechanisms mediating the motion perception of drifting isoluminant red–green gratings. We compare contrast thresholds for the detection and direction discrimination of drifting gratings (1.5 cpd), over a range of temporal frequencies (0.5–9 Hz) in the presence of variable luminance or chromatic noise. In the first experiment, we used dynamic luminance noise to show that direction thresholds for red–green grating motion are masked by luminance noise over the entire temporal range tested, whereas detection thresholds are unaffected. This result indicates that the motion of nominally isoluminant red–green gratings is mediated by luminance signals. We suggest that stimulus-based luminance artifacts are not responsible for this effect because there is no masking of the detection thresholds. Instead we propose that chromatic motion thresholds for red–green isoluminant gratings are mediated by dynamic luminance artifacts that have an internal, physiological origin. We have termed these “temporal chromatic aberration”. In the second experiment, we used dynamic chromatic noise masking to test for a chromatic contribution to red–green grating motion. We were unable to find conclusive evidence for a contribution of chromatic mechanisms to the chromatic grating motion, although a contribution at very high chromatic contrasts cannot be ruled out. Our results add to a growing body of evidence indicating the presence of dynamic, internal luminance artifacts in the motion of chromatic stimuli and we show that these occur even at very low temporal rates. Our results are compatible with our previous work indicating the absence of a chromatic mechanism for first order (quasi-linear) apparent motion [Vision Res. 40 (2000) 1993]. We conclude that previous conclusions based on the motion of chromatic red–green gratings should be reassessed to determine the contribution of dynamic luminance artifacts.

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1. Introduction

In this paper we address the issue of the loss of motion perception in color vision. It has been known for some time that the perceived speed of isoluminant gratings is slower in comparison to that of their luminance counterparts, and their motion may appear to cease altogether for short periods (Cavanaugh, Tyler, & Favreau, 1984; Hawken, Gegenfurtner, & Tang, 1994; Livingstone & Hubel, 1987; Lu, Lesmes, & Sperling, 1999a; Morland, 1982; Mullen & Boulton, 1992a, 1992b; Troscianko & Fahle, 1988). A perceived slowing may

also be observed for flickering chromatic stimuli but is less marked (Henning & Derrington, 1994; Metha & Mullen, 1997). A deficit of motion perception for color vision is also supported by a report of the loss of apparent motion at isoluminance in random dot kinematograms (Ramachandran & Gregory, 1978).

On the other hand, it is clear that this loss of motion perception in color vision is not complete, especially for suprathreshold stimuli. Both the direction of motion of drifting sinewave gratings and the frequency of flicker can be discriminated at contrasts close to, although not at, detection threshold (Cavanaugh & Anstis, 1991; Derrington & Henning, 1993; Gegenfurtner & Hawken, 1995; Metha & Mullen, 1996, 1998; Metha, Vingrys, & Badcock, 1994; Mullen & Boulton, 1992a; Palmer, Mobley, & Teller, 1993). Furthermore, contrary to the earlier report of Ramachandran and Gregory (1978), others have reported that color contrast can support

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apparent motion for isoluminant red–green gratings (Cropper & Derrington, 1996; Dobkins & Albright, 1993). Since detectable motion for isoluminant stimuli has been reported so frequently, it is unlikely to be due to simple luminance artifacts in the stimuli, such as those arising from optical aberrations or an inadequately set isoluminance. Instead, we have to assume that some form of motion processing is available to color vision.

In an attempt to elucidate this issue and reconcile some of these contradictory findings, Baker, Boulton, and Mullen (1998) and Yoshizawa, Mullen, and Baker (2000) found that the contribution of chromatic mechanisms to motion processing depends on whether first order (quasi-linear) or second order (nonlinear) motion mechanisms are activated.² These studies used chromatic and luminance noise masking and found a double dissociation between the effects of these two types of noise on chromatic apparent motion. Stimuli were Gabor micropattern kinematograms presented in two-flash apparent motion. When the motion of chromatic stimuli was mediated by a first order (quasi-linear) motion mechanism it was masked by luminance noise but was relatively robust to chromatic noise, indicating that the motion of chromatic stimuli is carried by luminance mechanisms. On the other hand, when the motion of chromatic stimuli is mediated by second order (nonlinear) mechanisms it was masked by chromatic noise but not luminance noise, indicating that it is solely mediated by chromatic mechanisms. Since these masking results were specific to the discrimination of the direction of motion and did not apply to simple detection of the stimuli, they indicate that the dynamic luminance signals generated internally from the chromatic stimuli are selective to a first order motion pathway and do not mediate stimulus detection. The conclusions from this work are two-fold: (1) First order motion based on chromatic mechanisms is weak or absent, but instead the motion of chromatic stimuli can be mediated by dynamic luminance artifacts; (2) Second order motion based on chromatic mechanisms is unimpaired relative to its luminance counter-parts.

Both of these conclusions are supported by observations using other stimuli and conditions. First, the psychophysical evidence for the potential contamination of the motion and flicker of chromatic stimuli by luminance artifacts is wide ranging. Artifacts arise from wavelength dependent temporal delays in the luminance

pathway and have been reported for flickering colored lights (Cushman & Levinson, 1983; de Lange Dzn, 1958; Lindsey, Pokorny, & Smith, 1986; Swanson, 1994; Swanson, Pokorny, & Smith, 1987, 1988; Walraven & Leebeek, 1964), as well as moving chromatic gratings (Stromeyer, Kronauer, Ryu, Chaparro, & Eskew, 1995; Stromeyer, Chaparro, Tolia, & Kronauer, 1997; Stromeyer et al., 2000; Tsujimura, Shioiri, Hirai, & Yaguchi, 1999, 2000), and are believed to originate at an early subcortical stage in vision. These dynamic luminance artifacts are only apparent under first order motion conditions when motion signals genuinely based on chromatic mechanisms are weak or absent (Baker et al., 1998; Yoshizawa et al., 2000, 2003).

Second, evidence for robust nonlinear chromatic motion mechanisms comes from a variety of sources. Motion from chromatic second order stimuli (such as contrast modulations or beats) shows no deficit in comparison to equivalent luminance stimuli, suggesting the presence of robust chromatic motion mechanisms based on nonlinear spatial processing (Cropper & Derrington, 1994, 1996; Seiffert & Cavanaugh, 1999). This conclusion is also consistent with the demonstrations of unsigned³ chromatic motion obtained from grating stimuli presented in apparent motion (Dobkins & Albright, 1993, 1994; Gorea, Papathomas, & Kovacs, 1993; Morgan & Ingle, 1994; Papathomas, Gorea, & Julesz, 1991), since these too depend on a spatial nonlinearity in the motion pathway. Motion based on nonlinear chromatic motion mechanisms has also been reported by Lu, Lesmes, and Sperling (1999b). Since masking experiments using luminance and chromatic noise have revealed no dynamic luminance artifacts in the second order motion of chromatic stimuli, we assume these mechanisms to be genuinely chromatic (Baker et al., 1998; Yoshizawa et al., 2000, 2003).

The growing body of evidence showing the absence of first order motion mechanisms in color vision, coupled with the presence of dynamic luminance artifacts, calls into question the functionality of one of the most commonly used stimuli in color-motion research, the drifting or flickering isoluminant chromatic grating. In this paper we explore the nature of the mechanisms mediating the motion perception of drifting isoluminant red–green gratings. If first order motion is weak or absent in color vision, how is the motion of chromatic grating stimuli mediated? Does the presence of internally generated dynamic luminance artifacts contribute to the perceived motion of chromatic gratings, and if so, over what temporal range? Do chromatic mechanisms

² We use the term “second-order” to refer to processing that requires a highly nonlinear mechanism, in distinction to “first-order” processing, which could be accomplished with essentially linear filtering operations. Note that this usage differs from that of others (e.g. Cavanaugh & Mather, 1989; Julesz, 1981), who use the terms in an image-statistical rather than mechanism-based sense. See Baker and Mareschal (2001).

³ Signed chromatic motion produces motion correspondence based on the chromaticity of image sub-regions, consistent with detection by a linear motion process. Unsigned motion produces motion correspondence between borders regardless of the chromaticity of the sub region, consistent with detection by a nonlinear mechanism.

contribute to the detection of motion of isoluminant chromatic gratings? Despite the evidence already described, systematic studies of these issues have not been made. We address these questions using a dynamic noise-masking paradigm. Stimuli are drifting red–green chromatic gratings carefully set at the isoluminant point using a minimum motion method for each subject and condition tested. Two tasks are used; the detection of the grating stimulus (contrast detection threshold), and the discrimination of its direction of motion (contrast threshold for direction discrimination). To determine whether chromatic and/or luminance mechanisms mediate each of these tasks, contrast thresholds were measured in the presence of variable chromatic or luminance dynamic noise using the rationale that the masking of thresholds by luminance noise indicates the involvement of luminance processes, and threshold masking by chromatic noise indicates the involvement of chromatic processes. These noise-masking experiments were run over a range of temporal frequencies. Our results indicate that, although red–green isoluminant gratings are detected by chromatic mechanisms, dynamic luminance artifacts mediate their motion over a wide range of temporal frequencies, extending down to very slow drift rates and over a wide range of contrasts. We find little evidence for a contribution of chromatic mechanisms to red–green grating motion, except possibly at very high chromatic contrasts. These results urge caution when interpreting the results of motion thresholds for chromatic grating stimuli.

2. Methods

2.1. Apparatus and observers

Stimuli were displayed on an RGB monitor (Barco CCID 7751) driven by a graphics card (VSG2/2, Cambridge Research Systems) housed in a PC. The monitor frame rate was 150 Hz noninterlaced. The spatial resolution of the screen was 496×428 pixels, subtending $21.5^\circ \times 16.2^\circ$ at a viewing distance of 100 cm. The gamma nonlinearity of the luminance output of the CRT guns was corrected in look-up tables using the VSG calibration system (OptiCAL, Cambridge Research Systems). The VSG2/2 provides a contrast resolution of 12 bits. The chromaticities of the red and green phosphors (CIE coordinates of $x = 0.6229$, $y = 0.3403$, and $x = 0.2776$, $y = 0.5837$, respectively) were measured at the National Research Council of Canada using a Photo Research PR-700 PC Spectrascan. The blue gun was not used. The mean luminance of the stimulus was 6.24 cd/m^2 .

Three observers participated, two of whom were experienced psychophysical observers and authors (TY, KTM), and the other a naïve observer (RPP). All had

normal or corrected to normal acuity and normal color vision assessed using the Farnsworth-Munsell 100-Hue test.

2.2. Stimuli

Stimuli were horizontal isoluminant red–green sinusoidal gratings or yellow–black luminance gratings with a spatial frequency of 1.5 cpd presented in a Gaussian contrast envelope ($\sigma = 0.66^\circ$, truncated at 2.6°). Stimulus contrast was ramped on and off in a raised cosine envelope with a total duration of 1 s. The temporal frequency of the grating was varied between 0.75 and 9.0 Hz. Isoluminance was measured with a method of adjustment; observers varied the ratio of red and green mean luminances in the stimulus to find a perceived minimum in the drift rate of a single Gabor stimulus (stationary envelope, drifting presented continuously). Isoluminance was determined as the mean of 20 settings. Isoluminance was determined for each subject over a range of TFs and a fit made to the data.

Luminance or chromatic noise was superimposed on the test stimuli. The noise was spatially one dimensional and temporally dynamic with a flat spatial and temporal Fourier amplitude spectrum. The chromatic noise was filtered with a spatially lowpass filter (Butterworth digital filter, as detailed in Yoshizawa et al., 2000) to reduce possible luminance artifacts from chromatic aberrations. 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 screen contrast units. The stimulus and noise were frame interlaced on a frame by frame basis. The maximum stimulus contrast available was 28.9% ($= 100/2/\sqrt{3}$). The noise was presented for 50 ms before and after the stimulus presentation.

2.3. Procedure

Two types of contrast threshold were measured: thresholds for detection of the stimulus and thresholds for discrimination of its direction of motion. For the detection task, a standard 2AFC staircase method was used to vary contrast with presentation intervals separated by 900 ms. The subject indicated which of the two intervals contained the stimulus (the other was blank). For the direction discrimination task, a single presentation interval was used in a staircase procedure; the subject indicated in which of two directions (up or down) the stimulus was drifting. Each staircase was terminated after eight reversals, and an average of the last six reversals was calculated as contrast threshold. Plotted data points represent the mean of 3–5 threshold measurements with the standard deviation of the measurement.

3. Results

3.1. Masking of detection and direction discrimination thresholds by luminance noise

We measured threshold versus luminance noise-masking functions for both detection and discrimination of the direction of motion of the isoluminant chromatic gratings at three temporal rates (0.75, 3.0 and 9.0 Hz). Results are shown in Fig. 1 for two subjects.

Data have been fitted with a standard noise-masking function:

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

where P_t is the power of the test grating at threshold (proportional to c^2), P_i is the power of the internal noise, which limits performance in the absence of external noise (e.g. Burgess, Wagner, Jennings, & Barlow, 1981; Pelli, 1990), P_e is the power of the external noise (proportional to c^2), and K is a constant proportional to the sampling efficiency of the threshold.

The most striking observation from the results is the differential behavior of the detection and direction discrimination thresholds. In both subjects, chromatic grating detection thresholds are robust to the luminance noise mask, showing no increase at any noise contrast. This demonstrates that the detection of the chromatic grating is not mediated by luminance mechanisms and

confirms that threshold is mediated by chromatic mechanisms. The absence of cross masking of chromatic detection by luminance noise has been reported previously for relatively slow or static stimuli (Gegenfurtner & Kiper, 1992; Losada & Mullen, 1995; Sankeralli & Mullen, 1997). These results now confirm that chromatic mechanisms mediate detection even up to relatively high temporal rates of 9 Hz. Furthermore, the fact that chromatic detection thresholds are not masked by luminance noise indicates that the stimulus itself is effectively isoluminant for these conditions, without significant luminance contrast arising from chromatic aberrations or an inaccurately set isoluminant point.

In comparison, the masking functions for direction discrimination of chromatic gratings show a large masking effect of luminance noise, with threshold increases of up to 0.75 log units at the highest noise contrasts used. The fitted noise-masking function (Eq. (1)) is a reasonable fit to the data. These results are important because they reveal the involvement of luminance mechanisms in the direction discrimination task over a wide temporal range. They also show that chromatic and luminance mechanisms are involved differentially in the detection and motion processing of red–green chromatic gratings. The selective masking of motion thresholds by the luminance noise indicates that the luminance contribution is dynamic and most likely physiological in origin.

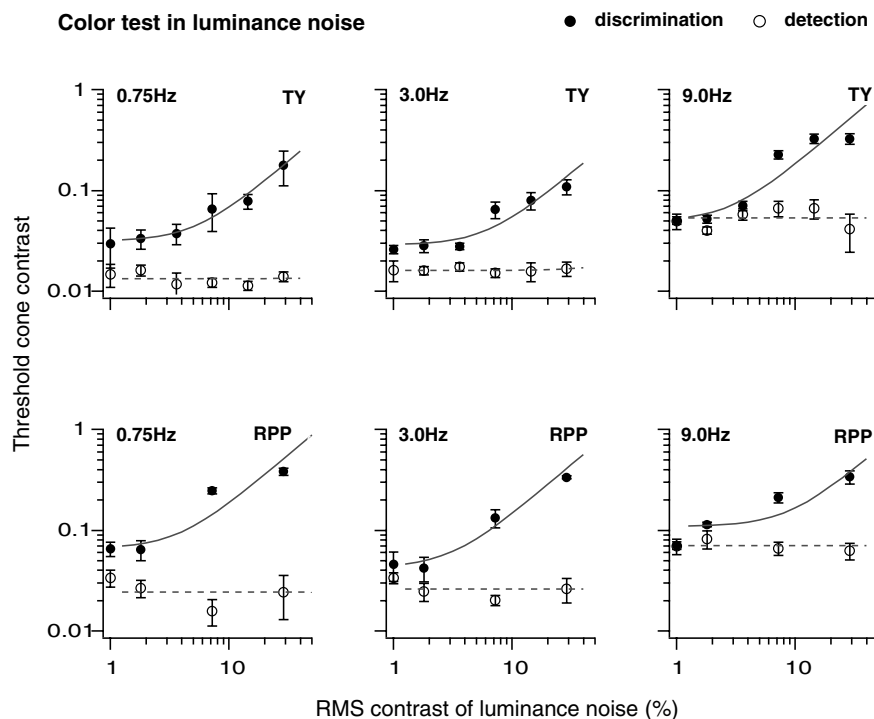


Fig. 1. Results for a red–green isoluminant test grating presented in dynamic luminance noise. Contrast thresholds are for detection (open circles) and direction discrimination (up versus down) (filled circles) in cone contrast units. The first plotted data point in each panel is for thresholds measured with no masking noise. The fit to the masking functions is given in the text (1). Data are for three temporal drift rates (0.75, 3.0 and 9.0 Hz) and are for two subjects. Error bars show \pm S.D.

As a control experiment we measured the effect of the luminance noise on the detection and motion discrimination of luminance gratings under the same conditions. Results are shown in Fig. 2. The fits of the standard noise-masking model to the data are good. Detection and direction discrimination thresholds both rise similarly with increasing noise contrast, although interestingly, both subjects show a small separation between detection and direction discrimination at 9 Hz. These results demonstrate the effectiveness of our noise as a mask for both types of threshold, and provide a template for the comparison for the effects of luminance noise on chromatic stimuli.

In order to illustrate the differential effect of the luminance noise on the two type of threshold across temporal frequency we have plotted our data in the form of temporal contrast sensitivity functions for different levels of masking noise contrast (Fig. 3). Even with no masking noise present (far left panels), detection and discrimination thresholds are not coincident, showing a small separation of between 0 and 0.2 log units typical of what has previously been reported in the literature (Cavanaugh & Anstis, 1991; Derrington & Henning, 1993; Gegenfurtner & Hawken, 1995; Metha & Mullen, 1996, 1998; Metha et al., 1994; Mullen & Boulton, 1992a; Palmer et al., 1993). At higher levels of luminance noise the gap between the detection and direction discrimination thresholds widens, reaching a log unit at the highest noise powers used (far right panels). These results demonstrate that the two thresholds are governed by separable processes; discrimination, which is

susceptible to luminance noise masking, and detection, which is not.

We plot the results of our control experiment using luminance stimuli in luminance noise in the same form (Fig. 4). Detection and discrimination thresholds remain closely linked, indicating that luminance-based mechanisms govern both. We note, however, that at the high powers of luminance noise (lower right panels) and at the high temporal frequencies, sensitivity for direction discrimination is poorer than for detection, suggesting a possible separation between discrimination and detection mechanisms within the luminance system at high temporal rates.

3.2. Masking of detection and direction discrimination thresholds by chromatic noise

While the results of Experiment 1 confirm the contribution of luminance processes to the direction discrimination thresholds of nominally isoluminant grating stimuli, they do not indicate the extent to which chromatic mechanisms may also be contributing. Direction discrimination could be based on the contribution of both chromatic and a luminance mechanism of differing sensitivities. To address this issue, we undertook masking experiments using chromatic noise.

Chromatic noise is a less useful tool than luminance noise because it is likely to be contaminated by luminance artifacts. Although we use spatially low-pass chromatic noise to reduce aberrations from optical sources (see Section 2), it is possible that some

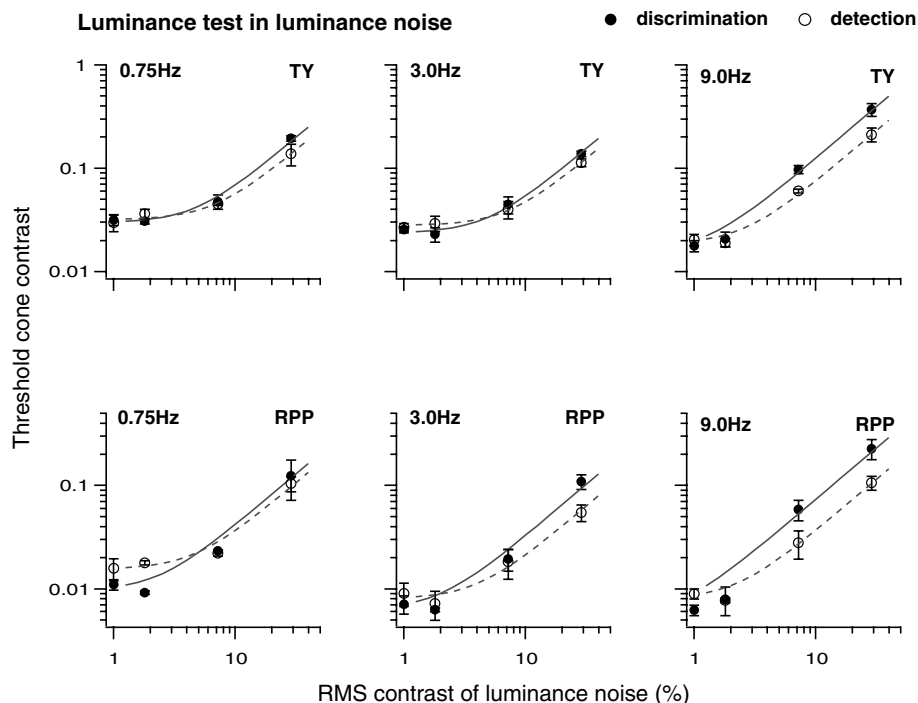


Fig. 2. Results for a luminance test grating presented in dynamic luminance noise. Other details are as for Fig. 1.

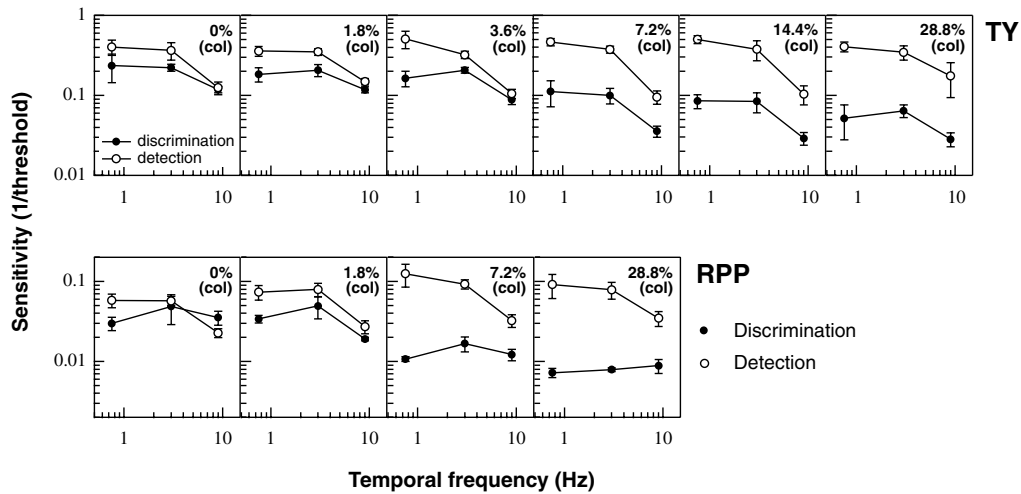


Fig. 3. Temporal contrast sensitivity functions for red–green isoluminant test gratings presented in dynamic luminance noise. The rms contrast (%) of the masking noise is given in the top right corner of each panel. Contrast sensitivity (cone contrast⁻¹) is plotted as a function of temporal frequency for detection (open circles) and direction discrimination thresholds (filled circles). Note that sensitivity to direction decreases at increasing levels of luminance noise, while sensitivity for detection remains constant. Data for two subjects. Error bars show \pm S.D.

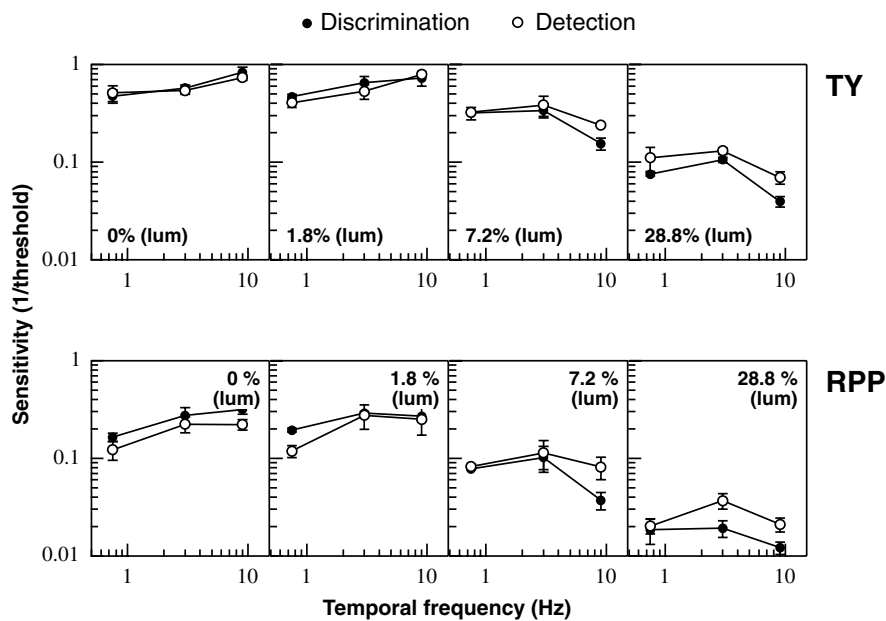


Fig. 4. Temporal contrast sensitivity functions for luminance test gratings presented in dynamic luminance noise. Details as for Fig. 3. Note that the direction and detection thresholds both decrease with increasing noise levels.

luminance contrast will remain. Moreover the dynamic nature of the chromatic noise is also likely to introduce luminance signals, as revealed in Experiment 1 above. In order to assess the amount of luminance artifact of either type in the chromatic noise, we undertook a control experiment in which we measure the capacity of the chromatic noise to mask luminance gratings. Results are shown in Fig. 5. The first point to note is that the chromatic noise has a masking effect on the luminance gratings at high noise contrasts that affects both detection and direction discrimination thresholds. A similar,

small amount of masking of the detection of luminance gratings by chromatic noise has been reported previously (Gegenfurtner & Kiper, 1992; Losada & Mullen, 1995; Sankeralli & Mullen, 1997) and suggests the presence of luminance contrast in the chromatic noise. A second point is that there is no differential effect of the chromatic noise on discrimination and detection thresholds, with a similar threshold elevation found for both. The absence of a selective masking of motion thresholds by the chromatic noise suggests that the masking effect found is mainly due to luminance arti-

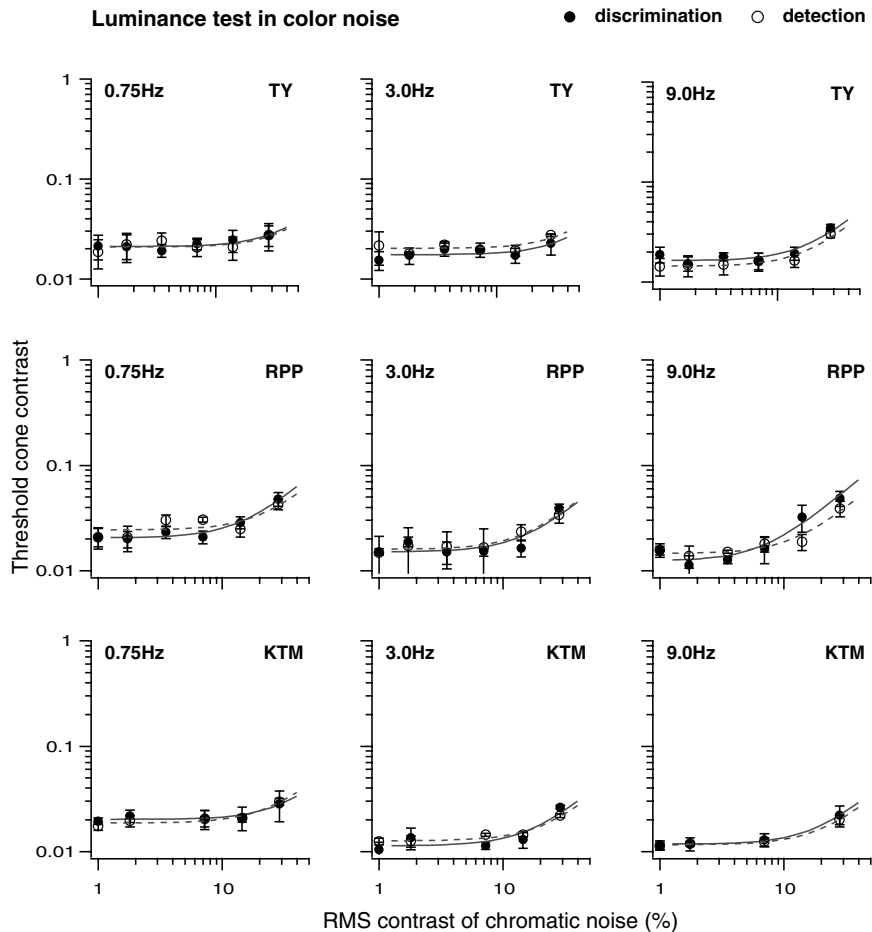


Fig. 5. Results for a red-green isoluminant test grating presented in dynamic chromatic (red-green) noise. Contrast thresholds are for detection (open circles) and direction discrimination (filled circles) in cone contrast units. The first plotted data point in each panel is for thresholds measured with no masking noise. The fit to the masking functions is given in the text (1). Data are for three temporal drift rates (0.75, 3.0 and 9.0 Hz) and are for three subjects. Error bars show \pm S.D.

facts in the chromatic stimulus rather than dynamic luminance artifacts, with discrimination thresholds elevated as a consequence of the elevation in stimulus detection threshold. For present purposes, however, the origin of the luminance artifact in the chromatic noise is not relevant.

In the next and main experiment of this section we measured the masking of the chromatic gratings by chromatic noise. Results are shown in Fig. 6. Detection thresholds for the chromatic gratings are strongly masked in the presence of the chromatic noise and are well fitted by the standard noise-masking function. Similar results have been reported previously (Gegenfurtner & Kiper, 1992; Losada & Mullen, 1995; Sanke-ralli & Mullen, 1997) and indicate that the detection of the chromatic gratings is mediated by chromatic mechanisms. This conclusion is also supported by the lack of masking of the detection thresholds by luminance noise shown in Fig. 1.

Of more interest is the effect of chromatic noise on direction discrimination. For one subject (TY), these

functions are relatively shallow showing a masking effect of chromatic noise confined to high noise contrasts, with the result that the gap between the detection and discrimination threshold closes at high contrasts. This may indicate a differential masking of detection and direction discrimination by the chromatic noise, and raises the possibility that chromatic processes are not involved in the direction discrimination task. For RPP and KTM, however, discrimination thresholds show a similar elevation to detection thresholds, with the gap between the two remaining similar at all contrasts.

The motion discrimination thresholds for chromatic stimuli are masked by the chromatic noise and the question is what is mediating this effect? Threshold elevation may be the consequence of residual luminance contrast in the chromatic noise (internal or stimulus-based) acting on luminance-based motion mechanisms, or it may reflect the action of chromatic noise on chromatic motion mechanisms. The presence of luminance contrast in the color noise was indicated by the control experiment of Fig. 5, and we already know from

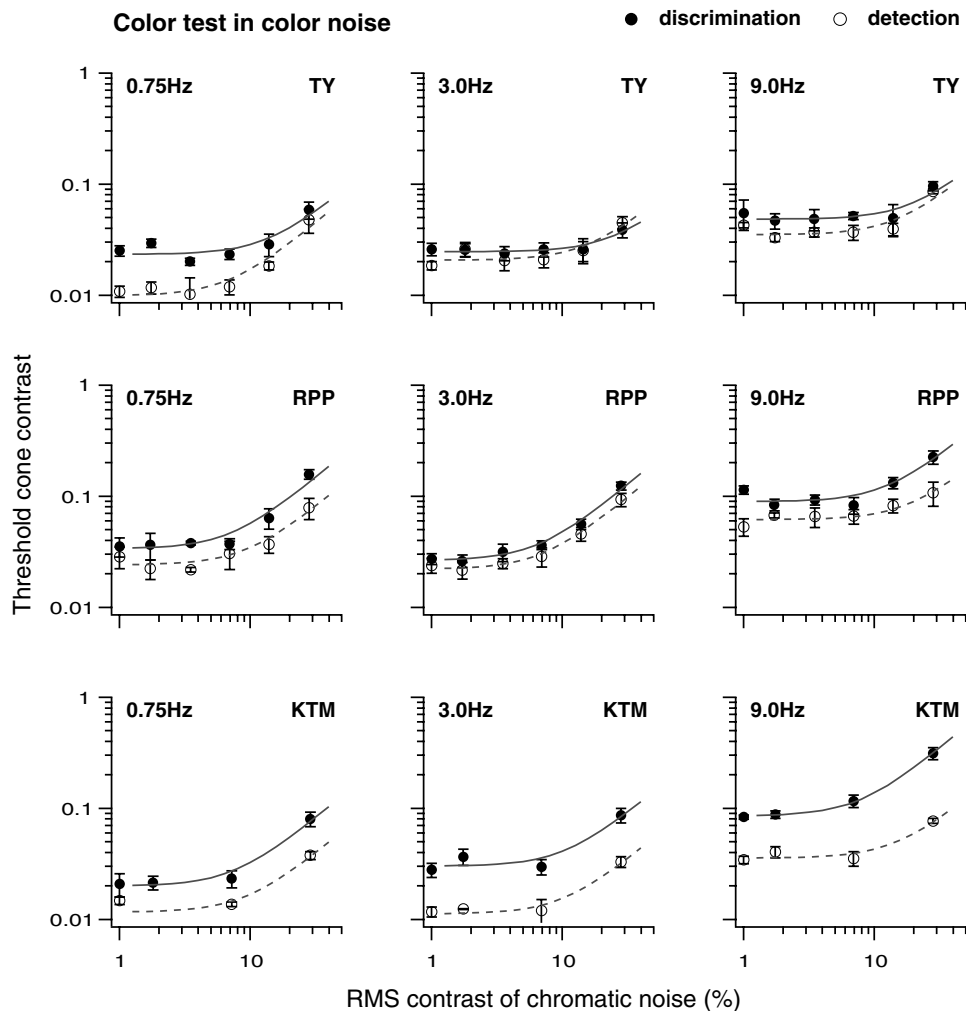


Fig. 6. Results for a red-green isoluminant test grating presented in dynamic chromatic (red-green) noise. Details as for Fig. 5.

Experiment 1 that it will elevate motion thresholds for chromatic stimuli. To assess its contribution quantitatively, we compare direction discrimination thresholds obtained for luminance test stimuli in chromatic noise (Fig. 5) to those for chromatic test stimuli in chromatic noise (Fig. 6). The comparison is shown in Fig. 7. The two data sets have been matched at the threshold obtained for zero noise by matching thresholds for the luminance test to those for the chromatic test. The solid line fits the direction discrimination thresholds for the luminance test stimuli and so provides a metric for the masking action of any artifactual luminance contrast in the chromatic noise. In other words, greater threshold elevation for the chromatic (filled symbols) than the luminance (hollow symbols and fit) test stimuli would indicate a masking effect of the noise that is genuinely chromatic in origin. Overlapping data sets, however, would indicate that artifactual luminance contrast in the chromatic noise entirely accounts for the elevation of the direction discrimination thresholds of the chromatic stimuli. The figure indicates that the two data sets are

similar. In some instances there is a greater threshold elevation for the chromatic than the luminance test stimulus (e.g. 0.75 Hz (TY); 0.75 and 3 Hz (RPP); 0.75 and 9 Hz (KTM)) but these effects do not seem to be systematic as there are also examples of the reverse effect (9 Hz, RPP) and of no effect. The excess of masking for the chromatic compared to luminance test stimuli was calculated for the highest noise contrast used and averaged over the three subjects: at 0.75 Hz it is 0.30 log units; at 3 Hz it is 0.15 log units; and at 9 Hz it is 0.25 log units. This gives an overall average excess of masking of the chromatic test of 0.24 log units. Thus even at the highest color noise contrast available all but 0.24 log units of the masking can be accounted for by luminance contrast in the color noise. At the lower noise contrasts used there was no significant difference between the masking of the chromatic and luminance test stimuli by the chromatic noise. Overall we conclude from these data that, at all except for the highest mask contrast available, there is no measurable effect of the chromatic noise on the motion of the chromatic test stimuli other

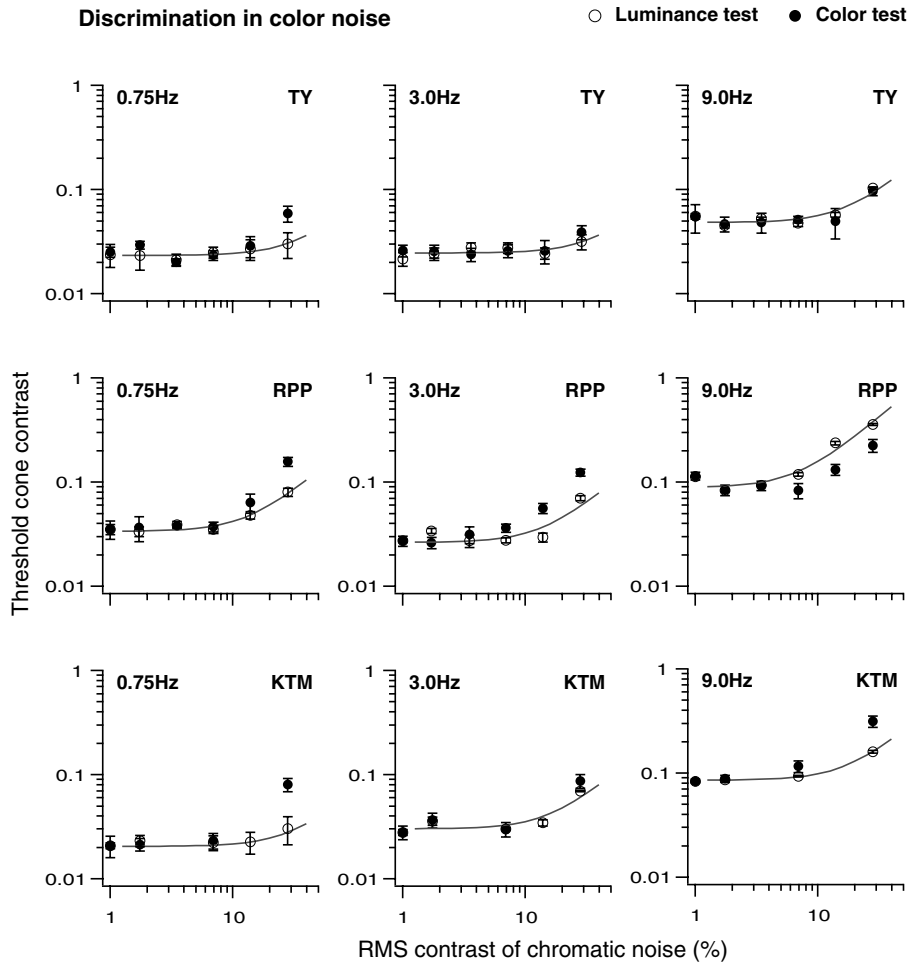


Fig. 7. Results comparing direction discrimination thresholds for a luminance test grating (open circles) and a red–green isoluminant test grating (filled circles) in red–green chromatic noise. Thresholds for the luminance test grating have been shifted up to match those for the chromatic test grating at the threshold for zero noise. The fitted curve is for the luminance test grating presented in color noise (Fig. 5), and gives a measure of the amount of masking generated by luminance artifact in the color noise. Any masking of the chromatic direction discrimination thresholds greater than predicted by this function may be attributed to the chromatic content of the mask. Error bars show \pm S.D.

than what can be accounted for by its luminance content.

4. Discussion

4.1. The contribution of luminance to chromatic grating motion

The key results of the paper demonstrate the effectiveness of luminance noise at masking isoluminant grating motion (Fig. 1), implying that the motion of this stimulus is mediated by luminance signals. The masking effect of luminance noise is selective for direction discrimination, and is absent for detection thresholds. This dissociation between detection and direction discrimination strongly suggests that the luminance “artifact” does not originate in the stimulus (e.g. from chromatic aberration, or an inaccurate isoluminant point), since

this would be expected to affect both types of threshold. The motion masking of the luminance noise was found to be just as strong at low temporal frequencies (0.75 Hz) as the high (9 Hz), revealing a surprisingly wide temporal range for the response of luminance mechanisms to isoluminant chromatic stimuli. In addition, for one subject (TY) we extended our measurements of chromatic threshold versus luminance noise to an even lower temporal frequency (0.5 Hz), and replicated the same result. Thus these results suggest that there is no lowest temporal frequency at which the artifactual luminance response can be eliminated. Because this luminance artifact is dynamic in nature we have termed it “temporal chromatic aberration”. Our results are compatible with a previous result revealing selective masking of chromatic grating motion (2 Hz) by a jittering (10 Hz) luminance grating mask (Stromeyer, Chaparro, & Kronauer, 1996). They also appear compatible with the results of Willis and Anderson (1998), who show that

adaptation to luminance gratings results in a reduced sensitivity for the direction discrimination, but not the detection of moving chromatic gratings.

Why would a moving red–green stimulus produce a response in a luminance pathway? Two possibilities emerge: differences in the temporal phase of the neural response to the component colors, or nonlinearities in the responses to the component colors or their summation. As mentioned in Section 1, wavelength dependent delays in the visual response to flicker are well established in the psychophysical literature (Cushman & Levinson, 1983; de Lange Dzn, 1958; Lindsey et al., 1986; Swanson, 1994; Swanson et al., 1987, 1988; Walraven & Leebeek, 1964). Delays between different chromatic components of a moving grating will produce relative phase shifts that potentially introduce a luminance “ripple” into the response to a nominally isoluminant stimulus. The psychophysical studies of Stromeyer et al. (1995, 1997, 2000) and Tsujimura et al. (1999, 2000) have demonstrated that temporal delays in the luminance system occur between stimulus components detected exclusively by L or M cones. These delays do not originate in the cones themselves, since they are found only in the luminance system and not in the M/L cone opponent system, but reflect delays between cone responses as they are combined into a luminance pathway. These delays can be sufficiently large to support a luminance direction discrimination threshold in an isoluminant chromatic grating (Fig. 6 of Stromeyer et al. (1997)). There is good evidence that the delay arises early in the visual system since it is monocular and applies to either flicker or motion. Moreover, similar effects have been measured in retinal magnocellular cells of primates (Smith, Lee, Pokorny, Martin, & Valberg, 1992), suggesting a likely M-cell origin. Stromeyer et al. (1997) have also proposed an M cell model of cone selective delays.

Nonlinearities in the responses of a luminance pathway to the component colors of a grating could also generate a luminance response to a moving chromatic grating. There is extensive physiological evidence for second harmonic distortions in the responses of retinal M (phasic) cells of the primate retina and LGN, which produce a frequency-doubled response to moving or flickering red–green chromatic stimuli even at isoluminance (Kaiser, Lee, Martin, & Valberg, 1990; Lee, Martin, & Valberg, 1989a, 1989b; Schiller & Colby, 1983; Valberg, Lee, Kaiser, & Kremers, 1992). The psychophysical identification of the frequency doubling effect has so far proved elusive (Cavanaugh & Anstis, 1991). This frequency-doubled response occurs over a wide temporal range (Lee et al., 1989a, 1989b) making it a candidate for the luminance response to chromatic gratings that we find psychophysically. Moreover, frequency doubling occurs at relatively high cone contrasts, which are reportedly above threshold for most cone

opponent P (tonic) cells (Lee et al., 1989a, 1989b), supporting the possibility that chromatic gratings are detected by a P cell pathway but their motion is mediated by the residual luminance response of an M cell pathway. An important caveat, however, is the observation outlined in Section 1 that dynamic luminance artifacts in chromatic stimuli are confined to linear (first order) motion and have not been found in nonlinear (second order) motion, making their origins in the frequency-doubled response of M cells less likely. In conclusion, further psychophysical experiments are required to determine whether dynamic luminance response to isoluminant red–green gratings arises from temporal phase lags, from a frequency-doubled response, or from some combination of the two.

4.2. Does color contribute to chromatic grating motion?

Our luminance noise-masking experiments reveal the contribution of luminance mechanisms to chromatic grating motion, but they leave open the possibility of a high threshold chromatic mechanism that could mediate motion at high chromatic contrasts. This contribution could appear as a flattening in the chromatic threshold versus luminance noise-masking function at high mask contrasts. Examination of the data in Fig. 1 is suggestive of some flattening of the direction discrimination thresholds for some of the conditions (e.g. TY at 9 Hz), however, this effect is not systematic and is not apparent under other conditions. These data thus leave open the possibility of a genuine chromatic contribution to motion at high chromatic contrasts.

As a direct test of a chromatic contribution to direction discrimination of chromatic gratings we performed the chromatic noise-masking experiment. Unfortunately, dynamic chromatic noise is limited in its usefulness because it is potentially contaminated by both optical chromatic aberration and the dynamic luminance artifact. The degree of luminance contamination of our chromatic noise was quantified in a control experiment, in which the effectiveness of the chromatic noise in masking a luminance test stimulus was measured. The results provided a masking template for the luminance component in the chromatic noise (Fig. 7). At low and middle chromatic noise contrasts all the masking motion thresholds for the chromatic gratings was predicted from the artifactual luminance contrast in the noise. At the highest chromatic noise contrast, however, we found masking of motion thresholds by chromatic noise that was not accounted for by its luminance content. This effect was small (0.24 log units), however, and was not systematic between subjects or conditions. We conclude that there is little evidence that chromatic mechanisms determine the motion thresholds for red–green isoluminant gratings, although the possibility remains open at high chromatic contrasts. In ad-

dition, these results discount the possibility of a motion response that is jointly sensitive to both color and luminance contrast, as suggested by Hawken et al. (1994).

There is a range of ways that chromatic mechanisms can make a potential contribution to motion thresholds. Previous studies have shown that color can contribute to motion via nonlinear motion processes, for example by using contrast modulations in the image (Baker et al., 1998; Cropper & Derrington, 1994, 1996; Yoshizawa et al., 2000), using unsigned chromatic borders (Dobkins & Albright, 1993), by using attention tracking (Cavanaugh, 1992) or position tracking strategies (Seiffert & Cavanaugh, 1999). Thus there is certainly a firm basis for the contribution of chromatic mechanisms to motion for the right type of stimulus. Although these diverse higher order processes are not excluded from contributing to the motion of sinewave gratings, their contribution is likely to be weak compared to that of first order (quasi-linear) motion processes. The absence of a first order motion process in color vision, as reported by Baker et al. (1998), Yoshizawa et al. (2000, 2003) is likely to account for why we find so little evidence for the contribution of chromatic mechanisms to chromatic grating motion. In conclusion, the evidence for robust higher order motion processes in color vision leaves the way open for a chromatic contribution to motion for other types of stimuli more suited to eliciting a higher order response.

4.3. Implications for other studies

Our results show that luminance signals determine motion discrimination thresholds for “isoluminant” red–green chromatic gratings over a wide temporal range (0.5–9 Hz) and over a wide range of chromatic contrasts. The spatial frequency range remains to be explored. These results raise important considerations for the use of red–green chromatic gratings in motion psychophysics, and suggest that these dynamic luminance artifacts may have contaminated previous results. Here we highlight two issues that have provided important evidence in the assessment of the parallel processing of color and motion that will now require reconsideration.

First, in Section 1, we cited many studies that have reported a small separation between thresholds for detection and direction discrimination of isoluminant chromatic gratings, and pointed out that this has been taken as evidence for color vision supporting motion thresholds. Here (Figs. 3 and 4) we have demonstrated that, once the luminance contribution to direction discrimination thresholds is eliminated by noise masking, the separation between detection and direction discrimination thresholds increases enormously (to around 1 log unit) and reaches the limits of the available stimulus contrast. Thus the contribution of chromatic

mechanisms to grating direction discrimination is weaker than previously thought, and may be absent altogether. This removes one of the previous arguments supporting the chromatic processing of motion, and provides evidence in favor of parallel color and motion processes. Secondly, previous results have reported a motion after effect from red–green isoluminant stimuli as evidence for a chromatic contribution to motion (Cavanaugh & Favreau, 1985; Derrington & Badcock, 1985; Mullen & Baker, 1985). This conclusion is now highly questionable, and will need to be reassessed to determine the artifactual luminance contribution to the measured “chromatic” motion after effect by using luminance noise to eliminate temporal chromatic aberration.

Our results in this paper suggest that over most of the contrast range the processing of the red–green isoluminant grating is split between two separate pathways: a static chromatic percept supporting detection, and an achromatic percept supporting motion. Mullen and Boulton (1992a) reported that even when direction could be reliably discriminated, the chromatic motion percept remained jerky until very high stimulus contrasts when it became smooth. The co-existence of two separable percepts (chromatic detection and achromatic motion) is likely to underlie the odd appearance of chromatic motion, which variously appears jerky, to “dance” from one direction to another, or can appear as a static colored pattern with a transparent ripple passing over a chromatic surface.

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