Absence of a chromatic linear motion mechanism in human vision

Tatsuya Yoshizawa * , Kathy T. Mullen, Curtis L. Baker Jr.

Department of Ophthalmology (H4-14), McGill Vision Research, McGill University, 687 Pine Avenue West, Montreal, Que., Canada H3A 1A1

Abstract

We have investigated motion mechanisms in central and perifoveal vision using two-frame random Gabor kinematograms with isoluminant red-green or luminance stimuli. In keeping with previous results, we find that performance dominated by a linear motion mechanism is obtained using high densities of micropatterns and small temporal intervals between frames, while nonlinear performance is found with low densities and longer temporal intervals [Boulton, J. C., & Baker, C. L. (1994) *Proceedings of SPIE*, *computational vision based on neurobiology*, *2054*, 124–133]. We compare direction discrimination and detection thresholds in the presence of variable luminance and chromatic noise. Our results show that the linear motion response obtained from chromatic stimuli is selectively masked by luminance noise; the effect is selective for motion since luminance noise masks direction discrimination thresholds but not stimulus detection. Furthermore, we find that chromatic noise has the reverse effect to luminance noise: detection thresholds for the linear chromatic stimulus are masked by chromatic noise but direction discrimination is relatively unaffected. We thus reveal a linear 'chromatic' mechanism that is susceptible to luminance noise but relatively unaffected by color noise. The nonlinear chromatic mechanism behaves differently since both detection and direction discrimination are unaffected by luminance noise but masked by chromatic noise. The double dissociation between the effects of chromatic and luminance noise on linear and nonlinear motion mechanisms is not based on stimulus speed or differences in the temporal presentations of the stimuli. We conclude that: (1) 'chromatic' linear motion is solely based on a luminance signal, probably arising from cone-based temporal phase shifts; (2) the nonlinear chromatic motion mechanism is purely chromatic; and (3) we find the same results for both perifoveal and foveal presentations. © 2000 Elsevier Science Ltd. All rights reserved.

Keywords: Color; Motion; Nonlinear; Linear; Luminance noise; Chromatic noise; Isoluminance

1. Introduction

The extent to which color vision is impaired at motion perception remains highly controversial. Early work high-lighted the deficiencies of the chromatic processing of motion, demonstrating the failure of isoluminant random dot kinematograms to generate a motion precept (Ramachandran & Gregory, 1978), the dramatic perceived slowing of drifting isoluminant gratings (Cavanagh, Tyler & Favreau, 1984; Livingstone & Hubel, 1987; Troscianko & Fahle, 1988; Mullen & Boulton, 1992a,b), and the failure to discriminate the direction of drift of gratings close to detection threshold (Lindsey & Teller, 1990; Cavanagh & Anstis, 1991; Mullen & Boulton, 1992b; Derrington & Henning, 1993; Metha, Vingrys & Badcock, 1994; Metha &

Mullen, 1998). Despite these demonstrations, however, it has become clear that color vision still retains substantial motion processing capabilities, and recent research efforts, using a wide range of different stimuli and approaches, have been directed at documenting and understanding these.

One of the consistent recent results is that the extraction of motion from chromatic 'second order' stimuli (e.g. contrast modulations, or beats) show no motion deficit in comparison to their luminance counter-parts, suggesting the presence of robust chromatic motion mechanisms based on nonlinear spatial processing (Cropper & Derrington, 1994). These results are also consistent with the demonstrations of unsigned[1] chro-

---

* Corresponding author. Tel.: +1-514-8421231; fax: +1-514-8431691.

E-mail address: yoshi@vision.mcgill.ca (T. Yoshizawa)

[1] '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 subregions, consistent with detection by a nonlinear mechanism.

matic motion obtained from grating stimuli presented in apparent motion (Papathomas, Gorea & Julesz, 1991; Dobkins & Albright, 1993, 1994; Gorea, Papathomas & Kovacs, 1993; Morgan & Ingle, 1994), since these also depend on a spatial nonlinearity in the motion pathway.

The preservation of nonlinear chromatic motion was also demonstrated by Baker, Boulton and Mullen (1998). These authors used Gabor micropattern kinematograms (two-flash apparent motion of arrays of Gabor micropatterns) to reveal both linear and nonlinear motion mechanisms (Boulton & Baker, 1993a,b, 1994). With a short SOA and high micropattern density, the pattern of performance was dependent on the carrier in a manner predicted by a linear motion mechanism. Using a longer SOA and low micropattern density, however, performance could be obtained for much larger displacements related to motion of the envelope, which was indicative of a nonlinear motion mechanism (Boulton & Baker, 1993a,b, 1994).

In the Baker et al. (1998) study, red–green chromatic stimuli were superimposed with luminance noise to mask any luminance artifacts that might intrude at isoluminance. The results suggested that color vision retains a nonlinear motion process comparable to that found for the equivalent luminance stimuli. On the other hand, the linear motion mechanism was found to be weak at isoluminance, and was virtually impossible to isolate in the presence of the luminance noise, suggesting the intrusion of dynamic luminance artifacts. As Baker et al. (1998) pointed out, a number of interesting questions emerged from this result.

One issue is that the extreme weakness of the chromatic linear motion mechanism is seemingly in conflict with the results of other studies that have reported a 'signed' chromatic motion percept (Papathomas et al., 1991; Dobkins & Albright, 1993, 1994; Gorea et al., 1993; Morgan & Ingle, 1994). Evidence for signed chromatic motion was provided by Cropper and Derrington (1996) using very briefly presented (17 ms), two-frame apparent motion with chromatic sinewave gratings. This study attempted to confirm the absence of any luminance artifacts in the chromatic stimuli by demonstrating a lack of masking by a luminance sinewave grating.

In this paper, we investigate the differences between the chromatic linear and nonlinear motion mechanisms more extensively. The main issue we consider concerns the role of the dynamic luminance noise on chromatic motion. A fixed level of masking noise was used for the chromatic linear motion condition by Baker et al. (1998) in order to remove the effects of any luminance artifacts. In this paper, we use varying levels of masking noise contrast and investigate its effects on detection and direction discrimination

thresholds for linear and nonlinear motion mechanisms for both chromatic and luminance stimuli.

We also investigate the effects of dynamic chromatic noise on our stimuli. As with the luminance noise, we measure the effects of variable contrast noise on detection and direction discrimination thresholds for chromatic and luminance stimuli under the linear and nonlinear motion conditions. The rationale for this is to determine the nature of the motion mechanism: selective masking of direction discrimination thresholds by luminance but not chromatic noise indicates a mechanism that is purely achromatic, whereas masking by both color and luminance noise suggests the mechanism is doing a double duty by receiving both types of input.

A secondary issue we consider is whether a foveal as opposed to perifoveal location of the stimuli is important for the relative strengths of linear and nonlinear motion. Baker et al. (1998) used two bands of Gabor kinematograms placed 6° above and below the fovea, whereas the other studies have generally used centrally fixated stimuli. We now make all our comparisons of the chromatic and luminance motion mechanisms using Gabor kinematograms presented both centrally and in the perifovea.

Our experiments reveal highly selective masking effects. Firstly we find that the linear motion obtained from the chromatic stimulus is masked by luminance noise, whereas nonlinear chromatic motion remains unaffected at all luminance noise contrasts. Critically, this effect is selective for motion since the luminance noise only masks direction discrimination thresholds, and not those for stimulus detection. Secondly, we find that chromatic noise has the reverse effect to luminance noise: linear motion from the chromatic stimulus is relatively (although not completely) unaffected by chromatic noise, whereas the nonlinear, chromatic thresholds are masked. Again these effects are selective for motion since they only occur for direction discrimination and not detection. We thus reveal a linear 'chromatic' mechanism that is susceptible to luminance noise and relatively unaffected by color noise. The parsimonious interpretation of these results is that linear motion obtained from isoluminant chromatic stimuli is based entirely on a luminance signal and has no chromatic input. We find that these effects occur equally for central and perifoveal vision.

In control experiments we confirm that the linear and nonlinear motion mechanisms can still be isolated with stimuli that are equated for their SOAs (and ISIs, and thus for their temporal frequency content), and in a separate experiment, using stimuli that are equated in their velocity. Under these conditions, the selective masking effects remain. These results indicate a genuine dichotomy between linear and nonlinear

motion with respect to chromatic stimuli, which does not arise secondarily from the choice of stimulus parameters used to isolate the two motion mechanisms.

2. Methods

2.1. Apparatus

All stimuli were displayed on an RGB monitor (Barco CCID 7751), driven by a graphics card (VSG2/2, Cambridge Research Systems) controlled by a PC. The spatial resolution of the screen was 496×428 pixels, subtending $21.5 \times 16.2°$ at a viewing distance of 100 cm; the monitor frame rate was 150 Hz, non-interlaced. The gamma nonlinearity of the luminance of the red and green CRT guns was corrected by look-up tables using the VSG calibration system (OptiCAL, Cambridge Research Systems), with a gun resolution of

12 bits, produced by a combination of two 8-bit palettes. 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/m².

2.2. Stimuli

The stimuli, illustrated in Fig. 1, were Gabor micropatterns presented in one horizontal band for foveal vision (A, B) or in two horizontal bands 6 degrees above and below the fovea for perifoveal vision (C, D), as described previously (Baker et al., 1998). Each band has two rows in which there are 3 or 7 Gabor micropatterns per row. The location of each micropattern was randomly jittered about a notional grid within the row.
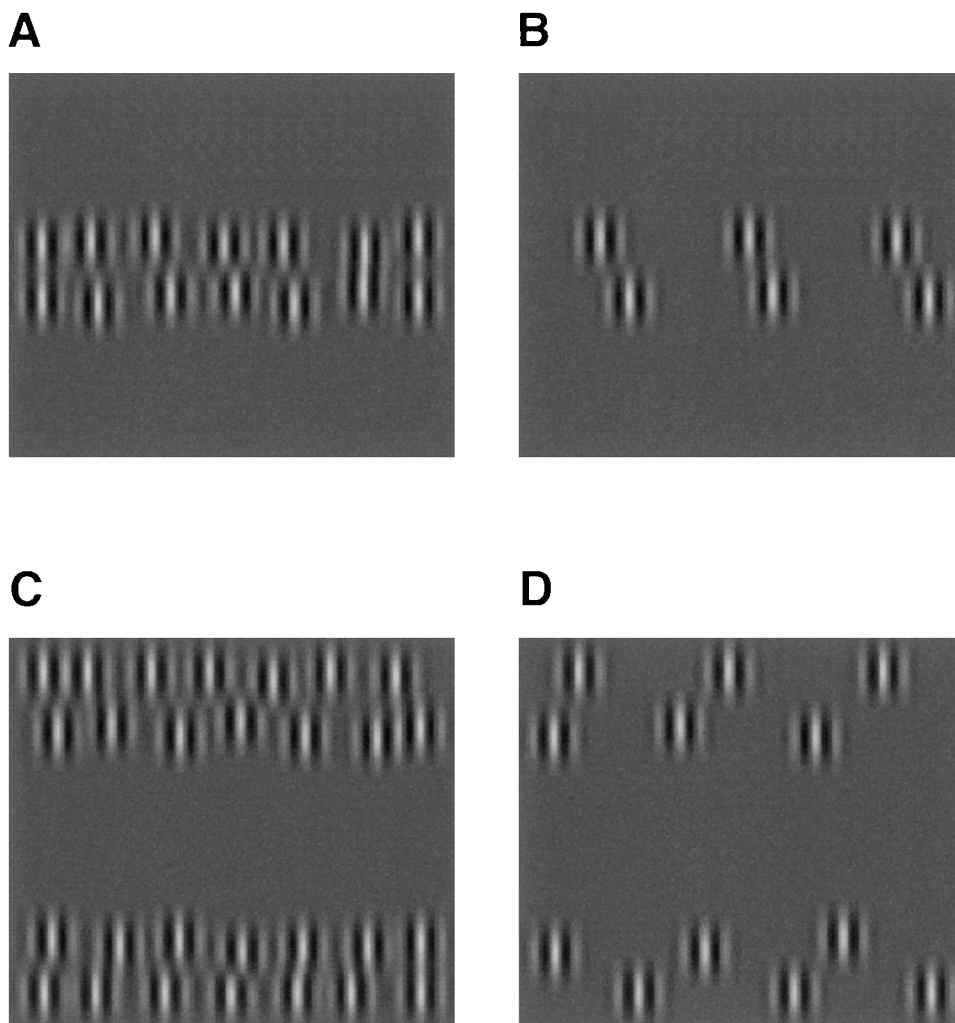

Fig. 1. Representative images in two-exposure Gabor micropattern kinematograms. Top (A & B) and bottom (C & D) panels are examples of stimuli for foveal and perifoveal vision, respectively. Left and right panels are for high and low density conditions used to isolate the linear and nonlinear mechanisms, respectively. The display size is $21.5 \times 16.2°$.

Each Gabor micropattern was the product of a carrier (a one-dimensional sine-wave grating) and an envelope (a two-dimensional Gaussian):

$$G(x, y) = C \exp[-(x^2/2\sigma_x^2 + y^2/2\sigma_y^2)]$$
$$\times \cos(2\pi(x \sin \theta + y \cos \theta)/\lambda) \qquad (1)$$

where θ is the orientation of the carrier, C is the contrast, σ_x and σ_y are the horizontal and vertical envelope width parameters, respectively, and λ is the spatial wavelength of the cosine wave (24 pixels, 1.0°); σ_x and σ_y were fixed at $3/4\lambda$. The dominant spatial frequency of 1 cpd is low enough to minimize any luminance artifacts from chromatic aberration (Flitcroft, 1989; Bradley, Zhang & Thibos, 1992).

The chromatic and luminance Gabor micropatterns have, respectively, counter-phase and in-phase red and green modulations:

$$r = r_{mean}(1 + G(x, y)) \quad \text{and} \quad g = g_{mean}(1 - G(x, y))$$

and

$$r = r_{mean}(1 + G(x, y)) \quad \text{and} \quad g = g_{mean}(1 + G(x, y))$$

where r_{mean} and g_{mean} are the mean luminances, and $G(x, y)$ is defined by formula (1).

Contrast is defined as the Michelson contrast $(L_{max} - L_{min})/(2*L_{mean})$, where L_{max}, L_{min}, and L_{mean} are maximum, minimum, and mean luminances, respectively, of the red and green modulations. The Gabor micropatterns were presented within a yellow surround of the same mean luminance and chromaticity $(r_{mean} + g_{mean})$. The CIE coordinates of the yellow surround for TY were $(x = 0.500, y = 0.449)$ in the fovea and $(x = 0.512, y = 0.439)$ in perifovea, and those for RPP were $(x = 0.522, y = 0.430)$ in fovea and $(x = 0.534, y = 0.419)$ in perifovea.

We used a minimum motion technique to determine the isoluminant points for each observer for both central and perifoveal vision. Observers adjusted the ratio of red and green mean luminances to find a perceived minimum motion of a single Gabor having a stationary envelope and a continuously drifting (2 Hz) 1 cpd carrier. Averages of 20 such determinations were made for foveal, superior perifoveal and inferior perifoveal stimuli; results for the two perifoveal stimuli were averaged. Despite setting the isoluminant point, some luminance signals may still potentially occur in the chromatic stimuli. These artifacts may arise because the stimuli were not temporally narrow band and there is a variation in the isoluminant point with temporal frequency (Cavanagh, MacLeod & Anstis 1987; Stromeyer, Kronauer, Ryu, Chaparro & Eskew, 1995; Metha & Mullen, 1996), or they may arise directly from temporal phase lags between L- and M-cone contrast signals (Swanson, Pokorny & Smith, 1987; Stromeyer et al., 1995; Stromeyer, Chaparro, Tolias &

Kronauer, 1997). In order to test for the presence of such residual luminance signals and to eliminate their impact, we determined the masking effect of superimposing luminance noise over the chromatic stimuli, and for comparison, the luminance stimuli.

The luminance noise was presented in alternating frames with the stimuli, and was extended 50 ms before and after the stimuli. The noise was dynamic, one-dimensional (vertical) with a flat spatial and temporal spectrum over the range allowed by the pixel size, display size, frame rate and presentation time. Noise amplitude was quantified as the rms contrast C_{rms}, the square root of the noise energy. For a uniform amplitude distribution, $C_{rms} = C/\sqrt{3}$, where C is the screen contrast. The maximum rms noise contrast that can be produced is 29% ($= 100/2/\sqrt{3}$) since the test stimuli and noise are presented in alternate frames. The chromatic noise was also spatially one-dimensional with a flat spatial and temporal spectrum, identical to that for the luminance noise. The chromatic noise was additionally spatially lowpass filtered with a Butterworth digital filter (Appendix A) to reduce luminance artifacts arising from optical chromatic aberration (Flitcroft, 1989; Bradley et al., 1992). This filter reduces amplitude by 40 dB at 4 cpd and has a cut-off frequency of 3 cpd. Chromatic amplitude was quantified as rms contrast, the same as for luminance noise, and the maximum averaged rms chromatic noise contrast was 14%. Note that the chromatic noise has less contrast energy because of the lowpass filtering.

2.3. Psychophysical procedure

Percent errors on the direction discrimination task were measured with a forced choice method; on each trial, one stimulus was presented and the subject indicated the direction of motion (left/right). At least 80 trials per condition were used, with the exact number given in each legend. When a noise mask was used, it onset 50 ms before the stimulus and offset 50 ms after the stimulus. A fixation point appeared briefly preceding each presentation.

Contrast detection thresholds for the luminance and chromatic stimuli were measured using a method of constant stimuli in a temporal two-alternative forced choice (2 AFC) task with the same temporal intervals as above. Four to seven values of contrast were used with 80 trials per contrast. A Weibull function was fit to the data and the 81.6% correct level taken as the threshold. Contrast thresholds for direction discrimination were measured in a single-interval forced-choice task, in which observers indicated the direction (left or right) of perceived motion. Thresholds were calculated in the same way as for detection threshold.
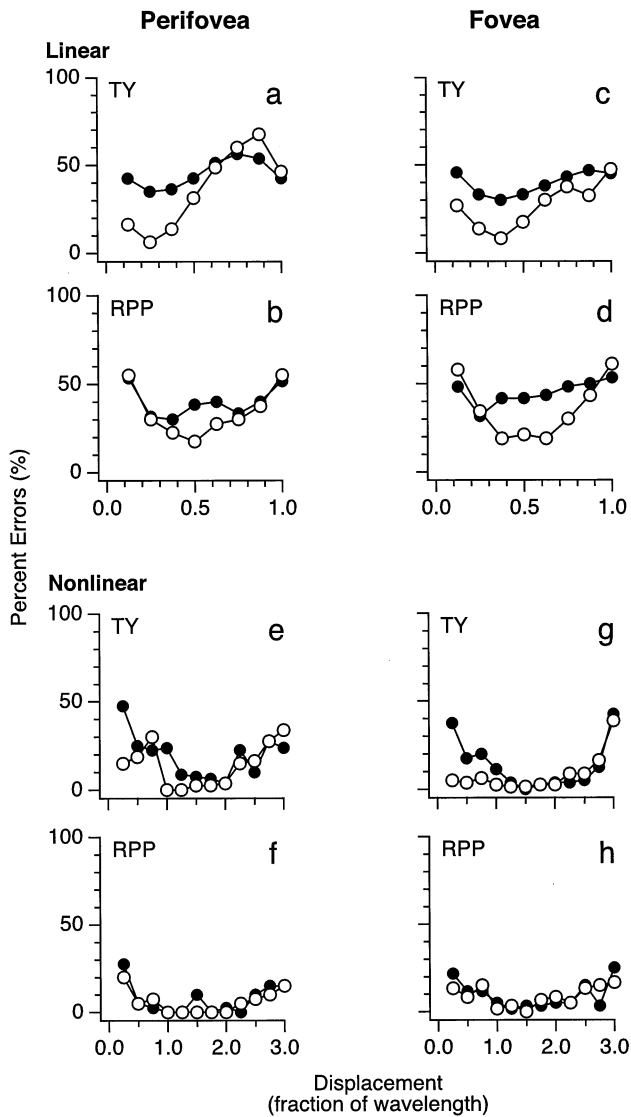
Fig. 2. Percent errors for direction discrimination as a function of displacement. Filled circles are for chromatic stimuli and open circles for luminance stimuli. Left panels are for the perifovea and right panels for the fovea. Stimuli were superimposed with luminance noise of 5.77 and 2.88% rms contrast for TY and RPP, respectively in the perifovea, and 4.33 and 1.44% rms contrast for TY and RPP, respectively in the fovea. The stimulus contrast was set to six times detection threshold. (Actual stimulus contrasts were as follows: (a) linear condition in the perifovea for TY, 15.0 and 40.0% for the luminance and chromatic stimuli, respectively; (b) same conditions for RPP, 14.3 and 44.8% for luminance and chromatic stimuli, respectively; (c) linear condition in the fovea for TY, 8.6 and 19.7% for the luminance and chromatic stimuli, respectively; (d), same conditions for RPP, 7.7 and 21.7% for luminance and chromatic stimuli, respectively; (e) nonlinear condition in the perifovea for TY, 23.3 and 40.0% for luminance and chromatic stimuli, respectively; (f) same conditions for RPP, 21.4 and 50.0% for luminance and chromatic stimuli, respectively; (g) nonlinear condition in the fovea for TY, 14.2 and 25.7%; for luminance and chromatic stimuli, respectively; (h) same conditions for RPP, 12.8 and 27.6% for the luminance and chromatic stimuli, respectively). Eighty trials per data point.

Detection and discrimination thresholds in the presence of the chromatic noise were measured by a staircase method in the two-alternative forced choice task. Observers indicated using the mouse buttons in which interval the stimulus appeared (detection task) or in which direction (left or right) the stimulus moved (discrimination task). Following an incorrect response the contrast was raised, and following two consecutive correct responses it was lowered in 1 dB steps. Each staircase terminated after eight reversals and the average of the last six reversals was taken as the threshold value. Each data point shows the average of at least five staircase measurements.

Observers viewed the stimulus monocularly with natural pupils in a dim room. All observers had normal color vision, as established by the Farnsworth–Munsell 100-Hue Test, and normal or corrected-to-normal acuity. One experienced (TY) and one naive observer (RPP) were used.

2.4. Treatment of noise masking data

We use noise simply as a test of whether or not threshold mechanisms have susceptibility to the contrast type of the noise mask. We have thus not fitted any noise model of detection (e.g. equivalent internal noise (Barlow, 1956)). Moreover, since in many cases the noise is ineffective right up to maximum screen contrast, no noise model can be applied.

3. Results

3.1. The isolation of linear versus nonlinear motion mechanisms

Apparent motion was produced by two successive stimulus exposures (100 ms) with a spatial displacement and an onset asynchrony (SOA). On the basis of previous work, we selected the spatial and temporal parameters of the stimuli to isolate either a linear or a nonlinear motion mechanism (Boulton & Baker, 1993a; Boulton and Baker, 1993b; Baker et al., 1998). A high density of micropatterns (seven per stimulus row, Fig. 1a,c), shifted left or right by $1/4\lambda$ (0.25°) with a short SOA (100 ms) are conditions which isolate a linear motion mechanism whose performance is related to the micropattern carrier. A low density of micropatterns (three per row, Fig. 1b,d), displaced by $3/2\lambda$ (1.5°) with a long SOA (150 ms) are conditions which reveal a nonlinear motion mechanism whose performance is related to motion of the micropattern envelopes.

In the first two experiments, we assess the effectiveness of these stimulus parameters for the isolation of the two motion mechanisms in both the fovea and the perifovea since in previous work only a perifoveal

stimulus presentation has been used (Baker et al., 1998). Fig. 2 shows percent errors in direction discrimination as a function of displacement in the perifovea (left column) and fovea (right column) under the conditions optimal for the linear (a–d) and nonlinear (e–h) motion mechanisms. All stimulus contrasts were set to six times their detection thresholds, and direction discrimination was measured in all conditions in the presence of a fixed level of suprathreshold luminance noise (Baker et al., 1998) which was used to reduce residual luminance signals in the chromatic stimuli. The effect of varying the level of luminance noise will be described later.

The primary purpose of these measurements was to verify that our choices of stimulus parameters were effective in isolating linear and nonlinear motion mechanisms for luminance stimuli, and secondarily to show for comparison the psychometric functions for chromatic stimuli. Linear models of motion detection (e.g. Adelson & Bergen, 1985) predict optimal performance at small displacements relative to the carrier wavelength (λ), with poor performance at larger displacements. Ideally a linear motion mechanism should give optimal motion at $1/4\lambda$ and chance performance at $1/2\lambda$; however, suprathreshold stimuli can be expected to recruit 'off-frequency looking', in which lower spatial frequency mechanisms contribute to the performance at larger displacements. Nonlinear motion mechanisms, however, respond to displacements of the envelope rather than the carrier, and thus show best performance at much larger displacements.

In the perifovea, using stimulus parameters designed to isolate linear motion (Fig. 2a,b), the results show that the percent errors for the luminance stimuli (open circles) reaches a minimum from $1/4$ to $1/2$ of a carrier wavelength (λ) with poor performance at larger displacements. (Note that error rates are not zero even for an optimal displacement, due to the superimposed luminance noise.) The small optimal displacement size and chance performance at larger displacements are compatible with detection by a linear motion mechanism. When chromatic stimuli (filled circles) were presented under the linear motion condition, performance collapses to near chance levels for observer TY and error rates are elevated for observer RPP, as shown previously for the perifovea (Baker et al., 1998).

Fig. 2c,d shows results for the linear condition in the fovea. The performance for luminance stimuli (open circles) once again approaches a minimum near a $1/4$ to $1/2\lambda$ of the Gabor carrier component. Again optimal performance at this small displacement is compatible with detection by a linear motion mechanism. For chromatic stimuli (filled circles), performance is again close to chance levels. Thus, we find no significant difference between the behaviour of our stimuli for foveal and perifoveal presentations: in both we find

linear motion for luminance stimuli and weakened linear motion responses for the chromatic stimuli.

Results for the nonlinear condition are shown in the bottom four panels of Fig. 2; note the 3-fold expanded abscissa scale. In the perifovea (Fig. 2e,f), direction discrimination has a broad range of optimal performance at much greater displacements ($1 - 2\lambda$) in comparison to the linear condition. Note the very different pattern, with very good performance at larger displacements (including 1λ), which gave chance performance in the linear condition, and worsening performance at smaller displacements below 1λ. This indicates detection by a nonlinear motion mechanism which responds to the stimulus envelope rather than the carrier. Similar functions are obtained in both fovea and perifovea. Similar functions are also obtained for both the luminance and chromatic kinematograms (open and filled circles), although performance was somewhat better for luminance stimuli at very small displacements. This overall result, that chromatic stimuli support only weak linear motion but robust nonlinear motion, has previously been reported for the perifovea (Baker et al., 1998) and these data suggest that it can be extended to include foveal stimulus presentations.

The displacements required for the best and worst performances on the motion task indicate that our choice of stimulus conditions effectively isolate linear and nonlinear motion mechanisms in both fovea and perifovea. As an additional confirmation of whether a linear or nonlinear mechanism determines foveal motion detection we performed a second experiment, in which we measured the ability to identify the direction of motion when the orientation of the Gabor carrier (θ in formula 1) was changed by 90° between the two exposures. The stimulus conditions were the same as before except for the 90° change in carrier orientation between exposures of the motion sequence. Changing orientation across successive exposures will abolish the response of a linear mechanism based on carrier motion, while preserving performance of a nonlinear mechanism which signals envelope motion (Baker et al., 1998).

Results are shown in Fig. 3. Under the linear condition (left panels), performance for both chromatic stimuli (filled circles) and luminance stimuli (open circles) was close to chance levels, indicating that motion perception is abolished by changing the carrier orientation. Results for the nonlinear condition (right panels) show that performance is still good; functions for both isoluminant stimuli (filled circles) and luminance stimuli (open circles) reach a minimum for displacements around 1.5λ. The results are consistent with those reported by Baker et al. (1998) for the perifovea and provide additional confirmation that our chosen parameters are adequate for the isolation of the linear and nonlinear motion mechanisms in both fovea and perifovea.
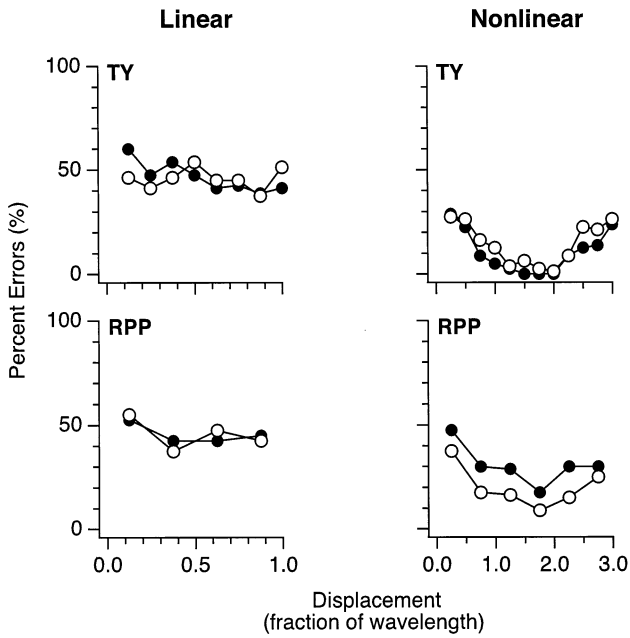
Fig. 3. The percent error of direction discrimination as a function of displacement when the carrier orientation of the Gabor micropattern is changed by 90° over two exposures. Filled and open symbols are for isoluminant and luminance stimuli. Luminance noise rms contrasts for observer TY and RPP are 8.66 and 4.33%, respectively. Eighty trials per data point. Foveal presentation.

3.2. The effect of luminance noise on chromatic and luminance motion

Since luminance noise only affects the detection of luminance contrast, and not the detection of isoluminant red–green stimuli (Gegenfurtner & Kiper, 1992; Losada & Mullen, 1995; Sankeralli & Mullen, 1997), superimposing luminance noise provides a tool for assessing the contribution of spurious luminance signals to performance with chromatic stimuli. In these experiments, we compare detection and direction discrimination thresholds for both luminance and chromatic stimuli in the presence of varying levels of superimposed luminance noise. Fig. 4 shows results for the fovea and Fig. 5 for the perifovea.

As a control experiment we first investigated the effects of the luminance noise on luminance-based motion perception with foveal presentations (as in Fig. 1a,b). Four left side panels of Fig. 4 show contrast thresholds for detection (open circles) and direction discrimination (filled circles) for luminance stimuli as a function of luminance noise rms contrast. The dashed lines show thresholds in the absence of noise. Error bars indicate the standard deviation estimated by a bootstrap method (Foster & Bischof, 1991; Efron & Tibshirani, 1993). Each estimated standard deviation is
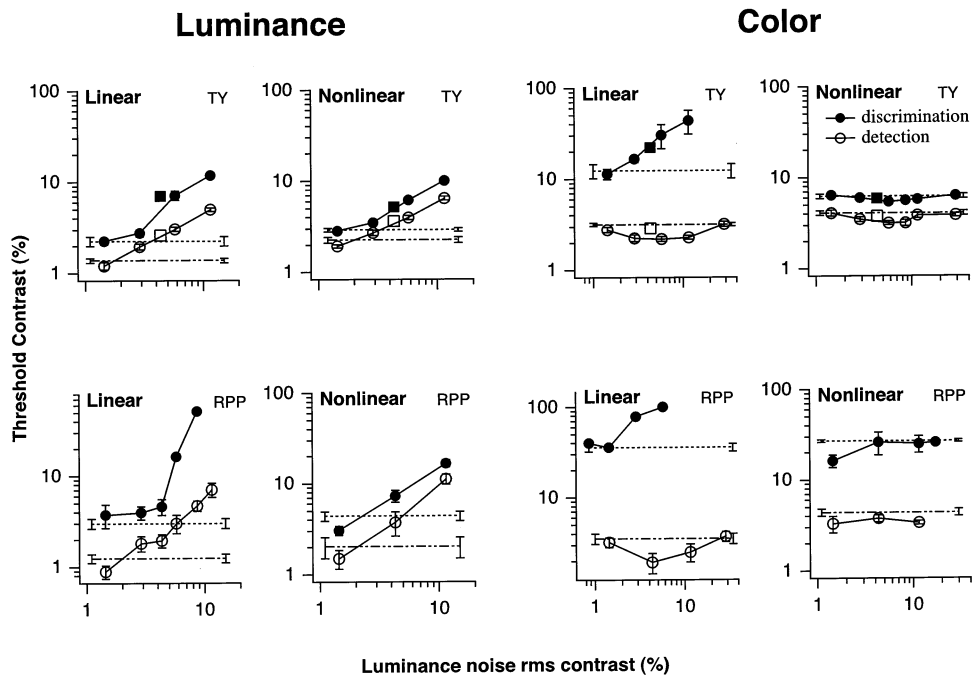

Fig. 4. Contrast thresholds for the direction discrimination of motion and stimulus detection for luminance Gabor micropatterns (left four panels) and chromatic Gabor micropatterns (right four panels) as a function of luminance noise rms contrast for foveal vision. Filled symbols represent the direction discrimination threshold and open symbols represent the simple detection threshold. Dashed and dot-dashed lines represent the direction discrimination threshold and the detection threshold in the absence of luminance noise, respectively. Top panels show results for linear and nonlinear conditions for observer TY and bottom panels are for RPP. In the top panels, squares are thresholds which are collected when both the direction discrimination and detection tasks are simultaneously done.
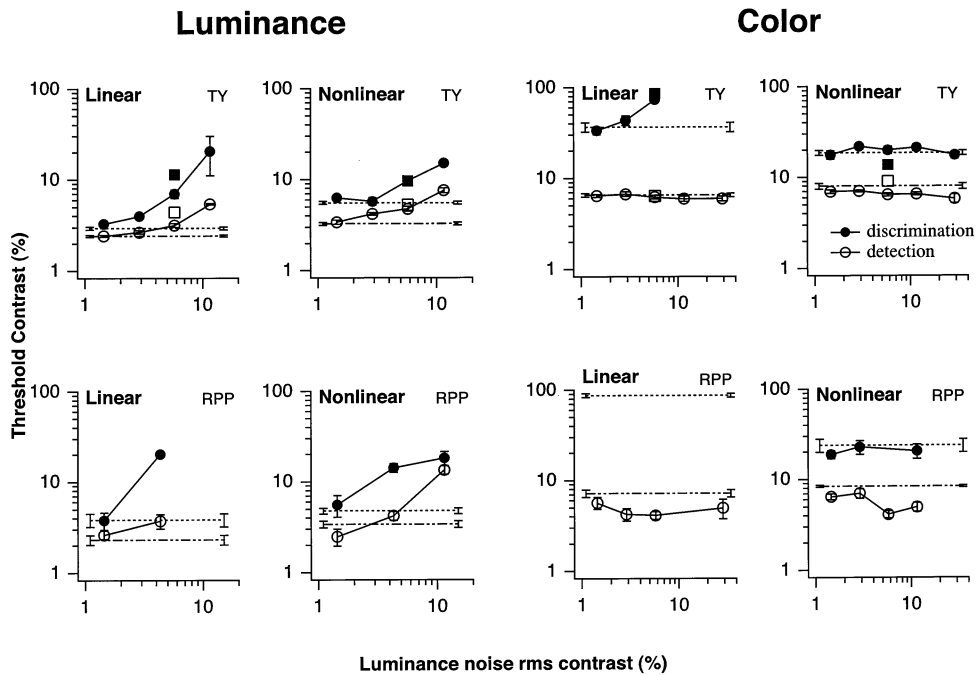
Luminance

Color

Fig. 5. Same as for Fig. 4, but for perifoveal stimuli.

obtained from 500 bootstrap samples. Under conditions optimal for both the linear and the nonlinear motion mechanism, the threshold functions for detection and direction discrimination increase together monotonically with luminance noise contrast. These results imply that the loss in motion discrimination occurs as a result of the increase in detection threshold; as the stimulus becomes harder to see the motion is harder to discriminate. These data are consistent with both detection and direction discrimination being mediated by a luminance mechanism.

The four panels on the right side of Fig. 4 show results of the experiments using red–green isoluminant stimuli. Chromatic detection thresholds are not elevated by the addition of luminance noise, replicating previous reports (Gegenfurtner & Kiper, 1992; Losada & Mullen, 1995; Sankeralli & Mullen, 1997) and confirming that our chromatic stimuli were truly isoluminant. Under conditions optimal for the linear mechanism (left panels), however, chromatic contrast thresholds for direction discrimination (solid symbols) increase markedly and systematically with luminance noise contrast. On the other hand, when the chromatic stimuli were presented with the optimal parameters for the nonlinear mechanism (right panels), direction discrimination thresholds are invariant with the luminance noise contrast up to maximum contrast. This result indicates that linear, but not nonlinear, chromatic direction discrimination is selectively impaired by the addition of luminance noise, and that this effect is not associated with a rise in detection thresholds, which remain constant in the presence of luminance noise. In other words, a loss

in linear chromatic motion occurs despite the fact that stimulus visibility is unaffected by the noise.

Previous studies of apparent motion with random Gabor kinematograms (Boulton & Baker, 1993a,b; Baker et al., 1998) used a perifoveal presentation (as in Fig. 1c,d) to minimize the possible contributions of non-motion mechanisms to performance. For comparison we repeated the above experiments in the perifovea. The four left panels of Fig. 5 show the detection and direction discrimination thresholds for luminance stimuli. Both the detection and direction discrimination thresholds under the linear and nonlinear motion conditions increase monotonically with luminance noise contrast, resembling the results found in the fovea (four left panels of Fig. 4) except that all the thresholds are uniformly higher for perifoveal viewing. Results for chromatic stimuli are shown in the right panels of Fig. 5. As before, chromatic detection thresholds are not elevated by luminance noise whereas direction discrimination thresholds under linear conditions are elevated. Note that for observer TY for linear chromatic motion, the full range of noise contrasts could not be used because direction discrimination thresholds reached the maximum chromatic contrast that our apparatus could present. For the same reason, observer RPP was unable to do the task at all for non-zero levels of luminance noise. The right panels show that under the nonlinear motion condition both the detection and direction discrimination thresholds for the chromatic stimuli remain invariant with luminance noise contrast right up to maximum contrast. Overall, the patterns of the data for perifoveal and foveal presentations are very similar.

It has been argued that when detection and direction discrimination thresholds are measured simultaneously, the observers' attention may be reduced for the second judgment and that this might account for the differences between detection and discrimination thresholds reported for chromatic stimuli (Derrington & Henning, 1993). Square symbols in Figs. 4 and 5 represent contrast thresholds obtained by a simultaneous temporal 2AFC. Observers indicated after each presentation firstly, which interval contained the stimulus and secondly, in which direction the stimulus moved. Results obtained for the simultaneous task show no systematic differences from thresholds obtained separately, indicating that a separation between these thresholds is not dependent on the method of measurement.

Fig. 6 summarizes our results by plotting the ratios of discrimination to detection thresholds as a function of luminance noise contrast for the data of Figs. 4 and 5.
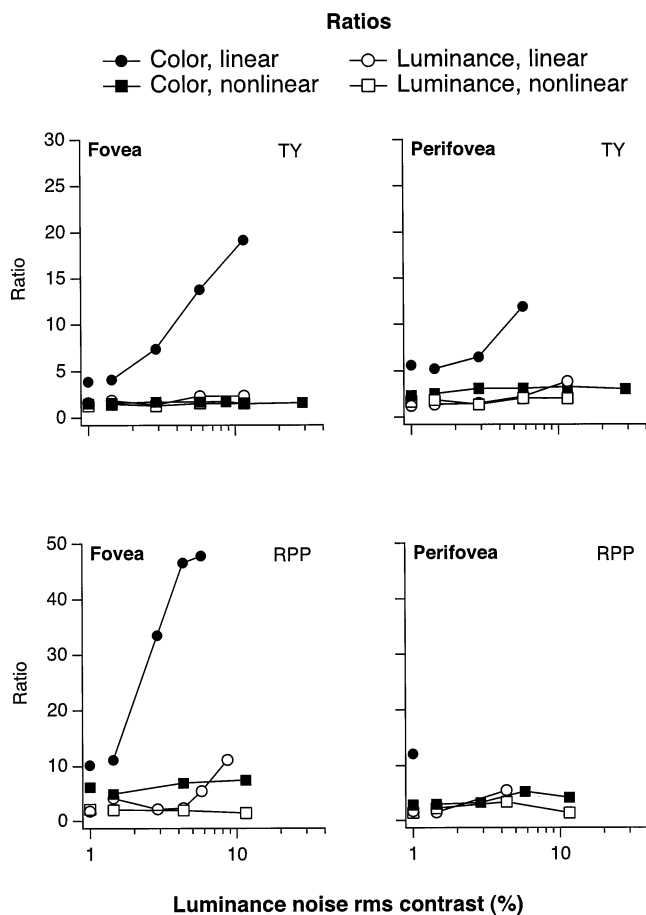

Fig. 6. Ratios of direction discrimination to detection thresholds as a function of luminance noise rms contrast in the fovea (left panels) and perifovea (right panels). The ratios for chromatic and luminance stimuli are shown by filled and open symbols, respectively. Circles and squares are for the linear and nonlinear conditions, respectively. Ratios for thresholds obtained in the absence of luminance noise are given by the unconnected points beside the ordinate. Some ratios for observer RPP were calculated using points which are linearly interpolated between the adjoining data points in Figs. 4 and 5.

Filled and open symbols are for chromatic and luminance stimuli, respectively. Left-hand panels are for the fovea and right-hand ones for the perifovea. In the fovea, the ratio for the linear chromatic motion condition (filled circles) increases steeply with luminance noise contrast, demonstrating the selective impact of luminance noise on direction discrimination but not detection thresholds. In the perifovea the same effect occurs, except that the ratio is measurable over a smaller range. However, the ratio for the nonlinear chromatic condition (filled squares) is flat at around 2 in the fovea and 3 in the perifovea for TY, and at around 7 in the fovea and 4 in the perifovea for RPP. These results are consistent with the robustness of both detection and discrimination thresholds against luminance noise for the nonlinear chromatic mechanism.

Ratios for the nonlinear luminance mechanism (open squares) are flat, indicating that detection and discrimination thresholds are equally affected by luminance noise. Ratios for the linear luminance mechanism (open circles), however, show a small increase with noise contrast in some cases (observer RPP, fovea), reflecting a somewhat steeper rise in direction discrimination thresholds with noise contrast than those for detection thresholds (Figs. 4 and 5). This effect is only noticeable in subject RPP, and is much (five times) smaller than the effect of luminance noise on chromatic stimuli. In an ANOVA described below we show it is not significant.

We investigated the significance of the differences in ratios between conditions using one-way and two-way repeated measures ANOVAs. Collapsing our data across noise contrast level, subject, and visual field location we performed a one-way repeated measures ANOVA to test the effect of condition (linear, nonlinear, colour, luminance) on ratios. A significant main effect of condition was found [$F_{(3,30)} = 10.9$, $P < 0.0001$]. Diffrences between conditions were further explored using a Tukey/Kramer post-hoc analysis which showed that the ratios for the chromatic linear condition are significantly higher than those for all other conditions at the 5% level. There are no significant differences among the nonlinear chromatic, linear and nonlinear luminance conditions. Using additional two-way mixed ANOVAs we confirmed that at the 5% level there were no significant differences between the two subjects, or between foveal and perifoveal presentations.

A gap between detection and direction discrimination thresholds of around 2–4-fold has been reported previously for isoluminant gratings in the fovea and near periphery (Lindsey & Teller, 1990; Cavanagh & Anstis, 1991; Mullen & Boulton, 1992b; Derrington & Henning, 1993; Palmer, Mobley & Teller, 1993; Metha et al., 1994; Metha & Mullen, 1998). This is broadly consistent with the values we report here for stimuli in
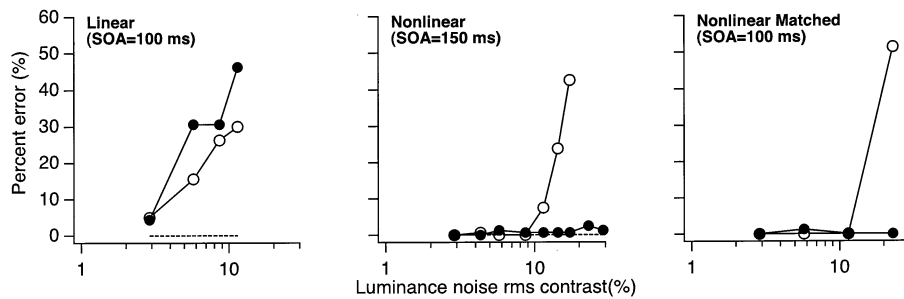
Fig. 7. The percent error of direction discrimination of motion as functions of luminance noise rms contrast. Filled and open symbols represent the percent error for isoluminant and luminance stimuli, respectively. Left, middle and right panels show the results for the linear, nonlinear and matched SOA conditions, respectively. Each data point is an average of 160 observations. Dashed lines in all panels show the percent error with no noise, and all are 0%. One hundred and sixty trials per data point. Foveal presentation.

the absence of noise, although we see a greater threshold gap for the chromatic linear stimuli than for the nonlinear ones. Previous studies, however, have not distinguished between linear and non-linear motion mechanisms and have not investigated the effects of added luminance noise.

3.3. Effects of SOA

We wondered whether the differing vulnerability to luminance noise which we find for our linear and nonlinear chromatic conditions might depend on the differing values of SOA which were used. For example, relative delays between L- and M-cone based signals can generate a luminance signal which is sufficient to support motion perception from chromatic stimuli (Swanson et al., 1987; Stromeyer et al., 1995). It is thus a possibility that a luminance signal might appear differentially for the different SOAs used in our stimuli.

To address this issue, we compared the effects of luminance noise on the two motion mechanisms under conditions in which the SOAs (and ISIs) were matched. We were unable to significantly increase the ISI for the linear motion condition without disrupting the linear motion process (Baker & Braddick, 1985; Georgeson & Harris, 1990; Boulton & Baker, 1993b). Instead, we reduced the SOA of the nonlinear condition (150 ms) to 100 ms to match that of the linear stimulus, while holding all other stimulus parameters the same. While this SOA is non-optimal for nonlinear motion, we could still obtain good nonlinear direction discrimination for low micropattern density and a large displacement (1.5λ).

Results are shown in Fig. 7 for both chromatic (filled symbols) and luminance (open symbols) stimuli in which percent errors in direction discrimination are plotted as a function of luminance noise contrast. We compare performance for the standard linear condition (left panel), the standard nonlinear condition (SOA = 150 ms, middle panel) and the matched nonlinear SOA condition (SOA = 100 ms). Under the linear condition,

the noise produces a loss in direction discrimination for both chromatic and luminance stimuli, as expected from the results described earlier (Figs. 4 and 5). Under both the nonlinear and matched SOA conditions, the direction discrimination of chromatic motion is not influenced by the luminance noise, while that of luminance motion is strongly impaired with increasing luminance noise contrast. These results demonstrate that the differing susceptibility of the two mechanisms to luminance noise is not simply due to the use of different values of SOA or differing temporal frequency spectra.

3.4. Effects of stimulus speed

Another possibility is that the differential effects of the luminance noise on the linear and nonlinear conditions might depend on stimulus speed. For example, Hawken, Gegenfurtner and Tang (1994) have proposed the existence of two chromatic motion mechanisms, one operative at low speeds (ca. 1 deg/s) which is purely chromatic, and one at higher speeds (ca. 8 deg/s) which is also sensitive to luminance contrast. Our linear stimulus conditions, which are susceptible to luminance noise, produce a relatively slow nominal speed of 2.5 deg/s, whereas our nonlinear conditions, which are insensitive to luminance noise, have a faster speed of 10 deg/s. Thus the results of Hawken et al. (1994) would predict that their fast color-luminance motion mechanism is detecting our slow linear chromatic stimulus, which seems unlikely. We nevertheless decided to assess the effect of stimulus speed on our findings.

We tested whether speed affects the isolation of the linear and nonlinear mechanisms and is a determinant of sensitivity to luminance noise by selecting combinations of displacement and SOA to produce both linear and nonlinear stimuli with the same intermediate velocity of 4.7 deg/s (see legend of Fig. 8 for details). The results of Fig. 8 (insets) demonstrate that a linear and a nonlinear motion mechanism can be separately isolated in the fovea under these matched-velocity conditions; percent errors in direction discrimination are plotted as

a function of displacement for chromatic (filled circles) and luminance (open circles) stimuli. Under both linear and nonlinear conditions, the psychometric functions obtained are similar to the corresponding functions under the standard conditions (right panels of Fig. 2) indicating effective isolation of the linear and nonlinear motion mechanisms.

Fig. 8 (main panels) compares the effects of luminance noise on direction discrimination for the linear and nonlinear conditions. Under the linear condition (left panel), percent errors in direction discrimination for luminance (open symbols) and chromatic stimuli (closed symbols) increases monotonically with luminance noise rms contrast, similar to results obtained under the linear condition in the matched-SOA experiment (left panel, Fig. 7). For nonlinear motion (right panel), direction discrimination thresholds are not affected for chromatic stimuli. Thus the effects of the noise remain selective for the linear chromatic motion and we conclude that differences in stimulus speed cannot account for the selectivity of the luminance noise.

3.5. The effect of chromatic noise

So far, we have shown that the linear chromatic motion is susceptible to luminance noise whereas the nonlinear chromatic motion is robust to it. The parsimonious interpretation of these results is that the linear 'chromatic' stimulus generates dynamic luminance signals that are sufficient to support direction discrimination, but not stimulus detection. This linear chromatic motion might be generated entirely by luminance cross-

talk via a mechanism that is essentially achromatic; alternatively, it might involve a dual mechanism that can carry both color and luminance signals. In this section we use chromatic noise to distinguish between these two possibilities: a mechanism that is masked by chromatic as well as luminance noise has dual color-luminance inputs, whereas a motion mechanism that is insensitive to chromatic noise is purely achromatic.

We thus repeated our masking experiments using chromatic noise. We measured detection and direction discrimination thresholds for chromatic and luminance stimuli under linear and nonlinear stimulus conditions, in the fovea and perifovea, as a function of chromatic noise contrast. Note that thresholds for luminance stimuli were included in order to assess whether the chromatic noise contains significant luminance artifacts. Fig. 9 shows the results for luminance (four left panels) and chromatic stimuli (four right panels) in the fovea. For luminance stimuli, detection (open circles) and direction discrimination (filled circles) thresholds both show a similar and slight rise as a function of chromatic noise rms contrast. In general, observer RPP shows a slightly greater effect than TY. There is no difference between the linear and nonlinear conditions. The slight elevation of thresholds for the luminance stimuli is probably caused by residual luminance artifact in the chromatic noise.

For chromatic stimuli, the linear condition indicates a differential effect of chromatic noise on detection and discrimination thresholds. Linear chromatic detection thresholds show a steep rise as a function of chromatic noise rms contrast, whereas direction discrimination thresholds show a smaller rise. For example, for RPP linear detection thresholds rise by 0.70 of a log unit whereas discrimination thresholds show no significant change up to the highest chromatic noise that can be produced. For TY, detection thresholds rise by 0.79 log units but direction discrimination rises by 0.37 log units. This result is consistent with stimulus detection being mediated by a chromatic mechanism since thresholds are strongly elevated by chromatic noise. Direction discrimination thresholds are much less sensitive or insensitive to chromatic noise compared to detection thresholds. We do, however, find an elevation of direction discrimination thresholds in TY; this could be caused by luminance artifacts present in the chromatic noise, since the existence of artifacts is indicated by the elevation of the luminance thresholds by the chromatic noise shown in the four left panels. Although less conclusive, these results are compatible with linear chromatic motion being produced by a luminance-based system, since direction discrimination thresholds are much less sensitive or insensitive to chromatic noise compared to detection thresholds. This conclusion is further supported by the perifoveal results shown below, and the statistics done on the data as a whole.
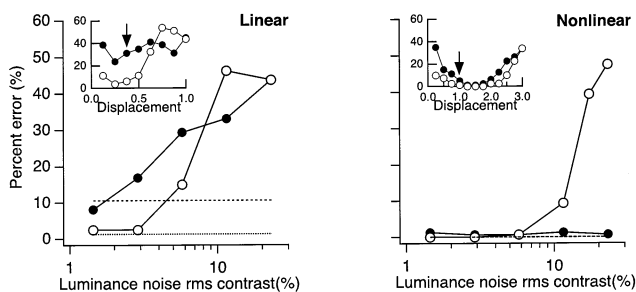

Fig. 8. Linear and nonlinear stimuli are matched in their velocities at 4.7 deg/s: exposure time is 80 ms, SOA for the linear and nonlinear conditions is 80 and 213 ms, respectively, and displacement is $3/8\lambda$ for the linear and λ for the nonlinear condition (as indicated by the arrow in the inset of each panel). Filled and open symbols show results for chromatic and luminance stimuli, respectively. Insets: percent error for direction discrimination as a function of displacement for the linear (left panel) and nonlinear (right panel) conditions. Main panels: percent error for direction discrimination as a function of luminance noise rms contrast for the linear (left) and nonlinear (right) matched velocity conditions. Dashed and dotted lines show percent errors in the absence of luminance noise for chromatic and luminance stimuli, respectively. Eighty trials per data point. Foveal presentation.

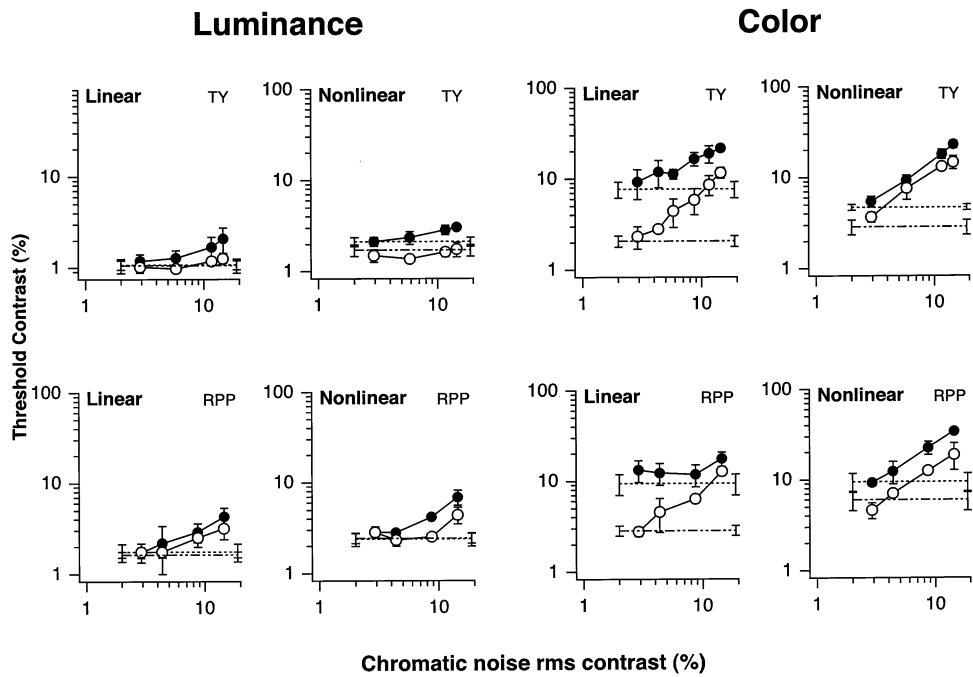**Luminance**   **Color**

Fig. 9. Contrast thresholds for direction discrimination of motion and stimulus detection for chromatic (left four panels) and luminance Gabor micropatterns (right four panels) as a function of chromatic noise rms contrast for foveal vision. Filled symbols represent the direction discrimination threshold and open symbols represent detection threshold. Dashed and dot-dashed lines show the direction discrimination and detection thresholds in the absence of chromatic noise, respectively. Top panels show the threshold functions for observer TY and bottom panels are for observer RPP. Error bars indicated ±1 SD.

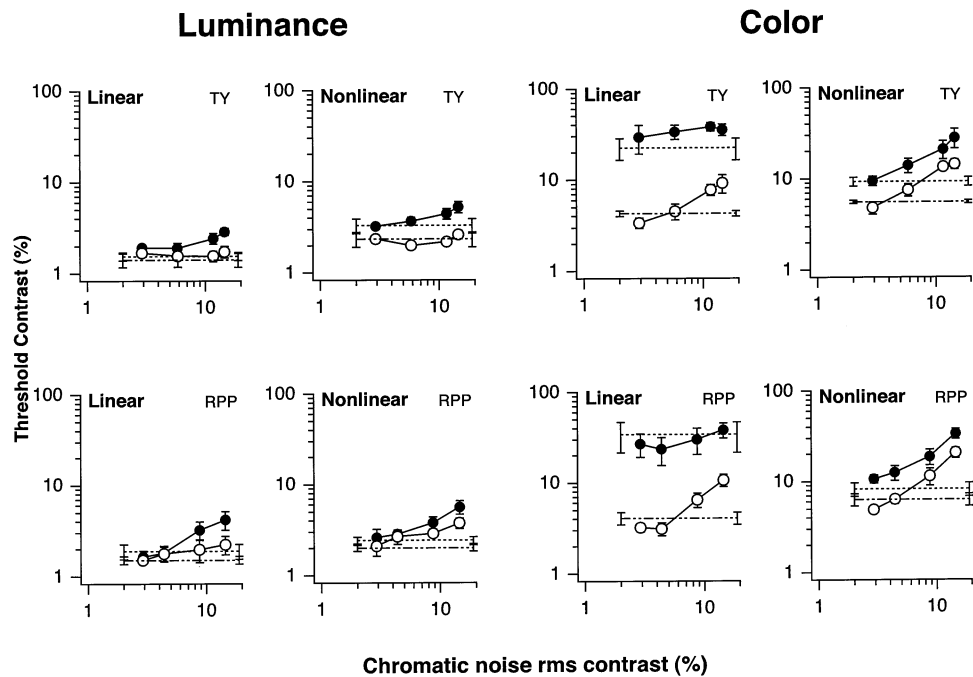**Luminance**   **Color**

Fig. 10. Same as for Fig. 9, but for perifoveal vision.

For the chromatic nonlinear condition, both detection and direction discrimination thresholds increase monotonically and in parallel with the chromatic noise contrast. This is consistent with the operation of a chromatic mechanism for both detection and direction discrimination.

We repeated these experiments for perifoveal viewing conditions and the results are shown in Fig. 10. The

effects of the chromatic noise on detection and direction discrimination thresholds for chromatic and luminance stimuli are similar to those in the fovea. For luminance stimuli, detection and direction discrimination thresholds are affected similarly by the chromatic noise showing a very slight rise at high noise contrasts, possibly arising from chromatic aberration in the chromatic noise. The linear and nonlinear conditions are affected similarly.

For chromatic stimuli, we again find a differential effect for linear and nonlinear stimuli. Detection of the chromatic linear stimulus is affected by the chromatic noise whereas the thresholds for direction discrimination are constant. The invariance of the direction discrimination thresholds with chromatic noise is clearer in the perifovea than the fovea, and supports the argument that linear chromatic motion is mediated by a luminance-based system. For the chromatic nonlinear stimuli, detection and discrimination thresholds rise in parallel as chromatic noise contrast increases up to its maximum value, suggesting

the involvement of chromatic mechanisms in both detection and discrimination.

In Fig. 11 we summarize the results of the effects of the chromatic noise by plotting the direction discrimination to detection threshold ratios. Filled and open symbols are for chromatic and luminance stimuli respectively. In both fovea (left panel) and perifovea (right panel), threshold ratios for linear chromatic motion (filled circles) decrease sharply as chromatic noise contrast increases, whereas the ratios for the nonlinear chromatic motion (filled squares) are unaffected by chromatic noise. This illustrates the selective effect of chromatic noise on detection by the linear mechanism.

The ratios for linear luminance motion (open circles) increase slightly with chromatic noise contrast, whereas ratios for the nonlinear luminance motion condition (open squares) have no systematic dependence on the chromatic noise. This illustrates that the chromatic noise has a slightly greater effect on linear luminance direction discrimination than detection, suggesting a better match of noise properties to the direction discrimination mechanism than to the detection mechanism. This effect was also observed for luminance noise (open squares in Fig. 6). In summary, our results show that the detection of the chromatic, linear stimulus is mediated by a chromatic mechanism, since thresholds are masked by chromatic noise but are insensitive to luminance noise. The motion of the chromatic stimulus, however, is mediated by a luminance-based mechanism, since direction discrimination thresholds are masked by luminance noise but are relatively insensitive to chromatic noise. The double dissociation of the effects of the chromatic and luminance noise allows us to discount the operation of a dual color-luminance mechanism for linear motion, since this would predict sensitivity to both color and luminance noise.

As in the case of Fig. 6, we investigated the significance of the differences in ratios between conditions using one-way and two-way repeated measures ANOVAs. Collapsing our data across noise contrast level, subject, and visual field location we performed a one-way repeated measures ANOVA to test the effect of condition (linear, nonlinear, colour, luminance) on ratios. A significant main effect of condition was found [$F_{(3,45)} = 21.6$, $P < 0.0001$]. Differences between conditions were further explored using a Tukey/Kramer post-hoc analysis which showed that the ratios for the chromatic linear condition are significantly higher than those for all other conditions at the 5% level. Using 2 way mixed ANOVAs we confirmed that at the 5% level there were no significant differences between subjects, or between foveal and perifoveal presentations.
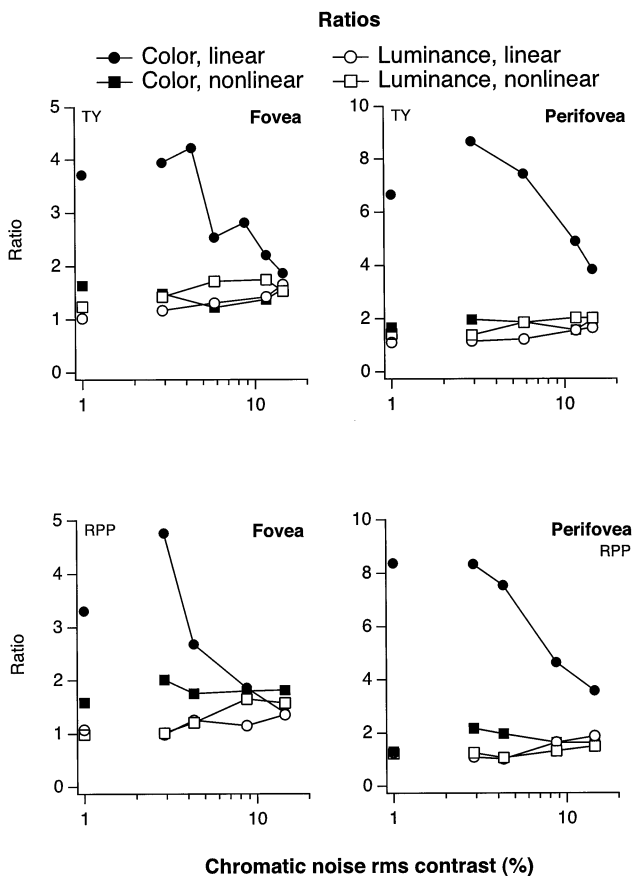

Fig. 11. Ratios of direction discrimination thresholds to detection thresholds as a function of chromatic noise rms contrast in the fovea (left panels) and perifovea (right panels). Results for chromatic and luminance stimuli are given by filled and open symbols, respectively. Circles and squares are for linear and nonlinear conditions, respectively. Ratios in the absence of chromatic noise conditions are given as unconnected points beside the ordinate.

4. Discussion

We have demonstrated that both linear and nonlinear motion mechanisms can be revealed in foveal vision using two-flash Gabor kinematograms. Our results have shown significant and highly differential effects in the masking of the linear and nonlinear mechanisms by chromatic and luminance noise. These effects concern the linear mechanism's response to chromatic stimuli and are generalized as follows: whereas detection thresholds are masked by chromatic noise but are robust to luminance noise, direction discrimination thresholds are masked by luminance noise and are robust to chromatic noise. The fact that the motion percept from a 'chromatic' linear stimulus can be eliminated by luminance noise, yet is unaffected by chromatic noise, demonstrates that this motion is based on luminance signals, probably via a cross-activation of the luminance system by the chromatic stimulus.

By contrast, when the nonlinear chromatic motion mechanism is isolated, neither detection nor direction discrimination thresholds are affected by luminance noise, yet both are equally affected by chromatic noise, indicating that this nonlinear motion mechanism is purely chromatic. This distinction between linear and nonlinear chromatic motion was found for stimuli presented in the central and perifoveal visual field.

We now further explore our claim that linear chromatic motion is mediated principally or entirely by luminance signals. Firstly, we require an understanding of the origins of the luminance information in the nominally chromatic stimulus. Secondly, we must be sure that the luminance signals are genuinely associated with the isolation of a linear motion mechanism and do not arise coincidentally from the particular stimulus parameters used for the isolation of linear and nonlinear motion.

4.1. Origin of the achromatic signals in chromatic linear motion

The achromatic signals originating from our chromatic stimuli selectively affect direction discrimination but not detection thresholds. They must have, therefore, a dynamic component and are unlikely to be accounted for by static artifacts arising from optical chromatic aberrations or a poorly measured isoluminant point. There is strong evidence to show that there are postreceptoral temporal delays between signals originating from the L- and M-cones, with L-cone based signals leading or lagging those of M-cones by 3–25 ms depending on stimulus parameters such as temporal frequency, background chromaticity and the individual subject (Swanson et al., 1987; Stromeyer et al., 1995). These delays can produce phase shifts (peaking around 7–9 Hz) large enough (ca $\pm 70°$), to generate a de-

tectable luminance signal in a nominally isoluminant moving stimulus (Stromeyer et al., 1995, 1997). Phase shifts only occur in the luminance mechanism and so can generate a luminance signal from a chromatic stimulus, but not a chromatic signal from a luminance stimulus. These postreceptoral phase shifts are likely candidates for the generation of the achromatic signals in our nominally chromatic stimuli. As our stimuli are presented abruptly and briefly rather than continuously, temporal delays would presumably produce transient luminance signals at the onset and offset of the spatial chromatic borders of the flashed stimuli, and these may be sufficient to produce a directional signal.

Stromeyer et al. (1997) have demonstrated that, under some conditions, detection of both chromatic and luminance moving gratings is mediated by a luminance mechanism. We find, however, that only direction discrimination and not detection was mediated by luminance cross-talk. We thus presume that our stimuli contain sufficient chromatic contrast to sustain detection, but insufficient to mediate motion. Since the most sensitive mechanism determines threshold, this indicates the presence of a sensitive chromatic detection mechanism but an absent or very insensitive chromatic linear motion mechanism that cannot be recruited even at maximum screen contrast.

One of the convenient features of the Gabor kinematograms is that the same type of stimulus can be used to reveal both the linear and nonlinear motion mechanisms. The separation between the two motion mechanisms is achieved by the choice of stimulus parameters: dense arrays of Gabors, presented with a short SOA (100 ms) in quadrature phase isolate a linear mechanism, whereas sparser Gabors with a longer jump size (> 1 cycle) and longer ISI (50 ms) reveal a nonlinear mechanism. The question arises, however, whether it is some aspect of these stimulus parameters that favours the intrusion of an internal luminance signal rather than the isolation of a linear or nonlinear motion mechanism per se. One possibility that we considered is whether the shorter SOA used in the linear condition might produce a stimulus more susceptible to the effects of cone-based temporal delays. We found, however, that if the SOA used for the nonlinear mechanism is shortened to match that of the linear one (with an ISI of 0), the nonlinear chromatic mechanism remains unaffected by the addition of luminance noise. In the light of the 'fast' color-luminance and 'slow' color-only mechanisms reported by Hawken et al. (1994), we tested the possibility that the stimulus speed is relevant to the intrusion of temporal delays. This factor is an unlikely candidate based on the nominal velocity of the linear and nonlinear stimuli: cone-based delays are reported to peak for grating stimuli drifting at around 7–9 Hz (Stromeyer et al., 1995), and this velocity corresponds better to our nonlinear stimulus (10 deg/s)

than to the linear one (2.5 deg/s). Nevertheless, we demonstrated that Gabor kinematograms presented with the same velocities could still be used to differentiate between a linear and nonlinear motion mechanism. Moreover, under these conditions, the susceptibility of the linear chromatic mechanism to luminance noise was unchanged. These results imply that the susceptibility to luminance noise is a genuine feature of the chromatic linear mechanism, rather than a coincidental correlate of the stimulus parameters chosen for its isolation.

4.2. Physiological basis of the motion mechanisms

There is good evidence from physiological experiments in macaque (Lee, Martin & Valberg, 1989; Smith, Lee, Pokorny, Martin & Valberg, 1992; Lee, Martin, Valberg & Kremers, 1993) and from psychophysical results (Stromeyer et al., 1997) that the phase shifts between the L- and M-cone-based signals originate in the primate M-cell pathway, probably at a retinal level. This pathway is associated with the responses of a luminance mechanism (Lee, Pokorny, Smith, Martin & Valberg, 1990; Merigan, Byrne & Maunsell, 1991; Merigan, 1992), hence providing the basis for achromatic signals to arise from a chromatic stimulus. It thus seems likely that the linear motion of our chromatic stimuli, which we have shown to be supported by luminance responses, utilizes the M-cell subcortical pathway, probably activating the same mechanisms as detect the luminance stimuli. The involvement of M-cells is supported by the high contrast gain and fast temporal characteristics previously reported for the achromatic linear mechanism (Boulton & Baker, 1994). However, since there is a considerable mixing of P- and M-cell inputs at the cortical level (e.g. Ferrera, Nealey & Maunsell, 1992, 1994), the linear motion mechanism need not be exclusively of P- or M-cell origin at the cortical level but might combine both inputs (De Valois & Cottaris, 1998).

The chromatic, nonlinear motion mechanism is robust against luminance noise at all contrasts and sensitive to chromatic noise, demonstrating that it is a purely chromatic mechanism. The P-cells are thought to be the subcortical origin of the red–green chromatic pathway (Schiller, Logothetis & Charles, 1990; Merigan, 1992), and so are likely to support this mechanism at the subcortical level. Any M-cell input must be small since this motion mechanism shows no susceptibility to luminance cross-talk.

4.3. Relationship to previous studies

Our conclusion, that we find no evidence for the existence of a color-only linear motion mechanism, is in contrast to various reports of 'signed' or linear motion for isoluminant stimuli (Dobkins & Albright, 1993;

Cropper & Derrington, 1996) and for non-isoluminant chromatic stimuli (Papathomas et al., 1991; Gorea et al., 1993; Morgan & Ingle, 1994). These previous studies have been done under a range of different conditions, and the results are not always easy to compare directly with our own study. One possibility that we had previously suggested was that signed chromatic motion may be more easily isolated with foveal presentations, as used in most other studies, compared to the perifoveal stimuli used by (Baker et al., 1998). This explanation, however, can now be dismissed since in the present study we find no significant differences between stimulus presentations in the fovea and perifovea.

It is possible that in these previous studies cone-based temporal phase shifts have affected the isoluminant stimuli. For example, Stromeyer et al. (1997) makes the point that under certain conditions it is impossible to eliminate luminance-based motion signals and produce a genuinely isoluminant stimulus. We presently do not know to what extent previous studies have been affected by such luminance cross-activation. The simplest test is to measure the effect of variable contrast luminance noise on the detection of the chromatic motion; only linear or 'signed' motion that is robust in the presence of luminance noise can be considered to be genuinely chromatic.

The study of Cropper and Derrington (1996) fulfills some of these criteria. A static luminance sinewave mask was shown to produce little effect on the direction discrimination of a chromatic grating presented in quadrature phase, suggesting motion detection by a signed chromatic mechanism. However, the mask was of relatively low contrast (around three times its own detection threshold) and higher luminance contrasts might produce more masking of the chromatic motion. Our Fig. 5 shows that we too find a linear chromatic motion response at low contrasts of the luminance noise mask, but that this response disappears as the mask becomes more suprathreshold. The results of Stromeyer, Chaparro and Kronauer (1996) have also shown a rather steep effect of luminance mask contrast on chromatic grating motion, especially at high mask contrasts. Thus a luminance mask of variable contrast is the best means of establishing whether a linear chromatic motion response arises from luminance signals. Until further replications are performed, it is difficult to know whether previous studies have isolated a purely chromatic signed motion mechanism.

Willis and Anderson (1998), using an adaptation paradigm, report that adaptation to counter-phasing luminance gratings affects chromatic direction discrimination, but not chromatic detection. These authors also report that adaptation to high contrast red–green isoluminant gratings increases direction discrimination thresholds for luminance test gratings (Anderson & Willis, 1996) supporting the idea that the chromatic

gratings, whether used as adaptation or as test stimuli, behave as if they activate a luminance-based motion mechanism. These results could also be interpreted in terms of cone-based phase lags generating a luminance ripple in the chromatic test grating. The effects also occur, however, at low temporal drift rates (1 Hz) at which the phase shift is very small at around 10° or less (Stromeyer et al., 1995, Fig. 16). Even at such low temporal rates, however, this phase shift still produces a plausible ISI for a motion mechanism (a phase shift of 10° at 1 Hz produces an ISI of 30 ms). Morgan and Ingle (1994) have also proposed that their 'signed' chromatic motion is combined with a luminance input to a common motion pathway. Both Willis and Anderson (1998) and Morgan and Ingle (1994) have argued in favour of a motion mechanism that is sensitive to both luminance and color contrast. In our case, this is specifically discounted by the fact that we find no motion mechanism that is sensitive to both chromatic and luminance noise. However, a motion mechanism that combines color and luminance contrast inputs under other stimulus conditions remains a possibility.

4.4. Implications of our study

Our results suggest that purely chromatic motion is mediated via a nonlinear mechanism, and that linear 'chromatic' motion is mediated by luminance cross-talk. We cannot, of course, preclude a chromatic linear motion mechanism that might be revealed using other stimuli or conditions. It is interesting to consider whether our conclusions can account for the many conflicting reports in the literature of both the losses and the retentions of chromatic motion. In general our results suggest that genuine failures of chromatic motion at isoluminance reflect the absence of a chromatic linear mechanism, whereas cases in which chromatic motion is robust may reflect the operation of a nonlinear chromatic mechanism, or cross-activation of a linear luminance mechanism. Many chromatic motion experiments have been performed using drifting grating stimuli whose motion is potentially supported by both linear and nonlinear motion mechanisms. For example, the loss of chromatic direction discrimination found near threshold (Lindsey & Teller, 1990; Cavanagh & Anstis, 1991; Mullen & Boulton, 1992b; Derrington & Henning, 1993; Metha et al., 1994; Metha & Mullen, 1998) may need to be reassessed to determine whether it reflects direction discrimination based on luminance cross-activation of a linear mechanism, or motion detection by a nonlinear chromatic mechanism. Motion after-effects, which have generally been tested with high contrast chromatic gratings (Cavanagh & Favreau, 1985; Derrington & Badcock, 1985; Mullen & Baker, 1985), may also reflect luminance cross-activation of linear chromatic motion, or the activation of a nonlin-

ear chromatic mechanism. Our finding that chromatic nonlinear motion is robust is consistent with the results of Cropper and Derrington (1994) who ascertain that chromatic motion can be obtained from non-Fourier stimuli and that, providing the contrast is not too high, drifting chromatic gratings may activate a nonlinear chromatic motion mechanism.

Appendix A

We implemented low pass spatial filtering with a recursive Butterworth low-pass filter. The magnitude function $|H(\omega)|$ of the Butterworth filter is defined as

$$|H(\omega)| = 1/\sqrt{\{1 + (\omega/\omega_c)^{2n}\}} \tag{A1}$$

where ω_c is the nominal cut-off frequency and n is the filter order. We chose parameters $\omega_c = 3$ cpd and $n = 14$ such that the magnitude function is at least 40 dB down at $\omega = 4$ cpd.

References

Adelson, E. H., & Bergen, J. R. (1985). Spatiotemporal energy models for the perception of motion. *Journal of the Optical Society of America, A, 2*, 284–299.

Anderson, S. J., & Willis, A. (1996). Parvocellular contribution to human motion perception. *Investigative Ophthalmology and Visual Science Supplement, 37*, 747.

Baker, C. L. Jr., Boulton, J. C., & Mullen, K. T. (1998). A nonlinear chromatic motion mechanism. *Vision Research, 38*, 291–302.

Baker, C. L. Jr., & Braddick, O. (1985). Temporal properties of the short-range process in apparent motion. *Perception, 14*, 181–192.

Barlow, H. B. (1956). Retinal noise and absolute threshold. *Journal of the Optical Society of America, 46*, 634–639.

Boulton, J. C., & Baker, C. L. Jr. (1993a). Different parameters control motion perception above and below a critical density. *Vision Research, 33*, 1803–1811.

Boulton, J. C., & Baker, C. L. Jr. (1993b). Dependence on stimulus onset asynchrony in apparent motion. *Vision Research, 33*, 2013–2019.

Boulton, J. C., & Baker, C. L. Jr. (1994). Psychophysical evidence for both a 'quasi-linear' and a 'nonlinear' mechanism for the detection of motion. In T. B. Lawton, *Proceedings of SPIE, computational vision based on neurobiology*, vol. 2054 (pp. 124–133).

Bradley, A., Zhang, X., & Thibos, L. N. (1992). Failures of isoluminance caused by ocular chromatic aberration. *Applied Optics*, *31*, 2109–2148.

Cavanagh, P., & Anstis, S. M. (1991). The contribution of color to motion in normal and color-deficient observers. *Vision Research*, *31*, 2109–2148.

Cavanagh, P., & Favreau, O. E. (1985). Color and luminance share a common motion pathway. *Vision Research*, *25*, 1595–1601.

Cavanagh, P., MacLeod, D. I. A., & Anstis, S. M. (1987). Equiluminance: spatial and temporal factors and the contribution of blue-sensitive cones. *Journal of the Optical Society of America*, *A*, *4*, 1428–1438.

Cavanagh, P., Tyler, C. W., & Favreau, O. E. (1984). Perceived velocity of moving chromatic gratings. *Journal of the Optical Society of America*, *A*, *1*, 893–899.

Cropper, S. J., & Derrington, A. M. (1994). Motion of chromatic stimuli: first-order or second-order? *Vision Research*, *34*, 49–58.

Cropper, S. J., & Derrington, A. M. (1996). Rapid colour-specific detection of motion in human vision. *Nature*, *379*, 72–74.

Derrington, A. M., & Badcock, D. R. (1985). The low level motion system has both chromatic and luminance inputs. *Vision Research*, *25*, 1879–1884.

Derrington, A. M., & Henning, G. B. (1993). Detecting and discriminating the direction of motion of luminance and colour gratings. *Vision Research*, *33*, 799–811.

De Valois, R. L., & Cottaris, N. P. (1998). Inputs to directionally selective simple cells in macaque striate cortex. *Proceedings of the National Academy of Sciences USA*, *95*, 14488–14493.

Dobkins, K. R., & Albright, T. D. (1993). What happens if it changes color when it moves?: psychophysical experiments on the nature of chromatic input to motion detectors. *Vision Research*, *33*, 1019–1036.

Dobkins, K. R., & Albright, T. D. (1994). What happens if it changes color when it moves?: the nature of chromatic input to macaque visual area MT. *Journal of Neuroscience*, *14*, 4854–4870.

Efron, B., & Tibshirani, R. J. (1993). *An introduction to the bootstrap*. Chapman & Hall.

Ferrera, V. P., Nealey, T. A., & Maunsell, J. H. R. (1992). Mixed parvocellular and magnocellular geniculate signals in visual area V4. *Nature*, *358*, 756–758.

Ferrera, V. P., Nealey, T. A., & Maunsell, J. H. R. (1994). Responses in macaque visual area V4 following inactivation of the parvocellular and magnocellular LGN pathways. *Journal of Neuroscience*, *14*, 2080–2088.

Flitcroft, D. I. (1989). The interactions between chromatic aberration, defocus and stimulus chromaticity: implications for visual physiology and colorimetry. *Vision Research*, *29*, 349–360.

Foster, D. H., & Bischof, W. F. (1991). Thresholds from psychometric functions: superiority of bootstrap to incremental and probit variance estimators. *Psychological Bulletin*, *109*, 152–159.

Gegenfurtner, K. R., & Kiper, D. C. (1992). Contrast detection in luminance and chromatic noise. *Journal of the Optical Society of America*, *A*, *9*, 1880–1888.

Georgeson, M. A., & Harris, M. G. (1990). The temporal range of motion sensing and motion perception. *Vision Research*, *30*, 615–619.

Gorea, A., Papathomas, T. V., & Kovacs, I. (1993). Motion perception with spatiotemporally matched chromatic and achromatic information reveals a 'slow' and a 'fast' motion system. *Vision Research*, *33*, 2515–2534.

Hawken, M. J., Gegenfurtner, K. R., & Tang, C. (1994). Contrast dependence of colour and luminance motion mechanisms in human vision. *Nature*, *367*, 268–270.

Lee, B. B., Martin, P. R., & Valberg, A. (1989). Sensitivity of macaque retinal ganglion cells to chromatic and luminance flicker. *Journal of Physiology*, *414*, 223–243.

Lee, B. B., Martin, P. R., Valberg, A., & Kremers, J. (1993). Physiological mechanisms underlying psychophysical sensitivity to combined luminance and chromatic modulation. *Journal of the Optical Society of America*, *A*, *6*, 1403–1412.

Lee, B. B., Pokorny, J., Smith, V. C., Martin, P. R., & Valberg, A. (1990). Luminance and chromatic modulation sensitivity of macaque ganglion cells and human observers. *Journal of the Optical Society of America*, *A*, *7*, 2223–2236.

Lindsey, D. T., & Teller, D. Y. (1990). Motion at isoluminance: discrimination/detection ratios for moving isoluminant gratings. *Vision Research*, *30*, 1751–1761.

Livingstone, M. S., & Hubel, D. H. (1987). Psychological evidence for separate channels for the perception of form, color, movement, and depth. *Journal of Neuroscience*, *7*, 3416–3468.

Losada, M. A., & Mullen, K. T. (1995). Color and luminance spatial tuning estimated by noise masking in the absence of off-frequency looking. *Journal of the Optical Society of America*, *A*, *12*, 250–260.

Merigan, W. H. (1992). P and M pathway specialization in the macaque. In A. Valberg, & B. B. Lee, *From pigments to perception* (pp. 117–124). New York: Plenum.

Merigan, W. H., Byrne, C. E., & Maunsell, J. H. (1991). Does primate motion perception depend on the magnocellular pathway? *Journal of Neuroscience*, *11*, 3422–3429.

Metha, A. B., & Mullen, K. T. (1996). Temporal mechanisms underlying flicker detection and identification for red–green and achromatic stimuli. *Journal of the Optical Society of America*, *A*, *13*, 1969–1980.

Metha, A. B., & Mullen, K. T. (1998). Failure of direction discrimination at detection threshold for both fast and slow chromatic motion. *Journal of the Optical Society of America*, *A*, *15*, 2945–2950.

Metha, A. B., Vingrys, A. J., & Badcock, D. R. (1994). Detection and direction discrimination thresholds for moving stimuli: the effects of color, luminance and eccentricity. *Journal of the Optical Society of America*, *A*, *11*, 1697–1709.

Morgan, M. J., & Ingle, G. (1994). What direction of motion do we see if luminance but not colour contrast is reversed during displacement? Psychophysical evidence for signed-colour input to motion detection. *Vision Research*, *34*, 2527–2535.

Mullen, K. T., & Baker, C. L. Jr. (1985). A motion after effect from an isoluminant stimulus. *Vision Research*, *25*, 685–688.

Mullen, K. T., & Boulton, J. C. (1992a). Interaction between colour and luminance contrast in the perception of motion. *Ophthalmic and Physiological Optics*, *12*, 201–205.

Mullen, K. T., & Boulton, J. C. (1992b). Absence of smooth motion perception in color vision. *Vision Research*, *32*, 483–488.

Palmer, J., Mobley, L. A., & Teller, D. (1993). Motion at isoluminance: discrimination/detection ratios and the summation of luminance and chromatic signals. *Journal of the Optical Society of America*, *A*, *10*, 1353–1362.

Papathomas, T. V., Gorea, A., & Julesz, B. (1991). Two carriers for motion perception: color and luminance. *Vision Research*, *31*, 1883–1891.

Ramachandran, V. S., & Gregory, R. L. (1978). Does colour provide an input to human motion perception? *Nature*, *275*, 55–56.

Sankeralli, M. J., & Mullen, K. T. (1997). Postreceptoral chromatic detection mechanisms revealed by noise masking in three-dimensional cone contrast space. *Journal of the Optical Society of America*, *A*, *14*, 2633–2646.

Schiller, P. H., Logothetis, N. K., & Charles, E. R. (1990). Functions of the colour-opponent and broad-band channels of the visual system. *Nature*, *343*, 68–70.

Smith, V. C., Lee, B. B., Pokorny, J, Martin, P. R., & Valberg, A. (1992). Responses of macaque ganglion cells to the relative phase of heterochromatically modulated lights. *Journal of the Physiology*, *458*, 191–221.

Stromeyer, C. F. III, Chaparro, A., & Kronauer, R. E. (1996). The color and motion of moving-colored patterns are processed independently? *Investigative Ophthalmology and Visual Science Supplement*, *37*, 916.

Stromeyer, C. F. III, Chaparro, A., Tolias, A. S., & Kronauer, R. E. (1997). Colour adaptation modifies the long-wave versus middle-wave cone weights and temporal phases in human luminance (but not red–green) mechanism. *Journal of the Physiology*, *499*, 227–254.

Stromeyer, C. F. III, Kronauer, R. E., Ryu, A., Chaparro, A., & Eskew, R. T. (1995). Contributions of human long-wave and middle-wave cones to motion detection. *Journal of the Physiology*, *485*, 221–243.

Swanson, W. H., Pokorny, J., & Smith, V. C. (1987). Effects of temporal frequency on phase-dependent sensitivity to heterochromatic flicker. *Journal of the Optical Society of America*, *A*, *4*, 2266–2273.

Troscianko, T., & Fahle, M. (1988). Why do isoluminant stimuli appear slower? *Journal of the Optical Society of America*, *A*, *5*, 871–880.

Willis, A., & Anderson, S. J. (1998). Separate colour pathways underlie the detection and discrimination of moving chromatic targets. *Proceedings of the Royal Society of London*, *B*, *265*, 2435–2441.