



# A Nonlinear Chromatic Motion Mechanism

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**Previous research has demonstrated two categorically distinct mechanisms mediating apparent motion of kinematograms composed of eccentricity-confined, randomly placed Gabor micro-patterns: a quasi-linear mechanism operating for high micropattern densities and short time separations, and a nonlinear mechanism operating at low micropattern densities or longer time separations. Here we compare the performance of these two mechanisms using color (isoluminant) and luminance-defined stimuli. When these stimuli are defined only by their color contrast, the response of the quasi-linear mechanism is severely impaired, while the nonlinear mechanism remains fully operative. This result further strengthens the dichotomy between the two kinds of motion perception, and suggests that when color vision supports motion perception it does so primarily, or perhaps entirely, via a nonlinear mechanism. © 1998 Elsevier Science Ltd**

Motion Color Linear Nonlinear Non-Fourier

## INTRODUCTION

A wealth of anatomical and physiological evidence suggests two distinct retinal-cortical processing streams in the primate visual system. A parvocellular-temporal cortex pathway, with a low temporal and high spatial passband, is thought to mediate primarily fine spatial acuity, form perception and color vision. A magnocellular-parietal cortex pathway, having a high temporal and low spatial passband, is thought to mediate motion perception (Zeki, 1978; Ungerleider & Mishkin, 1982; van Essen & Maunsell, 1983; Hubel & Livingstone, 1987; DeYoe & van Essen, 1988; Merigan *et al.*, 1991). A parallel processing of color and motion has been proposed as the basis of human psychophysical studies demonstrating that motion perception fails when stimuli are modulated in color but not in luminance. For example, the segregation of random dot kinematograms fails at isoluminance (Ramachandran & Gregory, 1978), and drifting color gratings appear to move more slowly than their luminance counterparts, or to be stationary (Cavanagh *et al.*, 1984; Livingstone & Hubel, 1987). However, this simple scheme has been challenged by demonstrations of good direction discrimination (e.g., Cavanagh & Anstis, 1991; Mullen & Boulton, 1992; Dobkins & Albright, 1993; Palmer *et al.*, 1993; Metha *et al.*, 1994; Cropper & Derrington, 1996) and motion aftereffects (Cavanagh & Favreau, 1985; Derrington &

Badcock, 1985; Mullen & Baker, 1985; see also Wohlgenuth, 1911) from isoluminant stimuli, and a report of motion-nulling between pairs of gratings of varying luminance and chromatic content (Chichilnisky *et al.*, 1993).

A persistent issue in these studies is whether isoluminant stimuli, though designed to stimulate selectively chromatic (color-opponent) mechanisms, might inadvertently also stimulate luminance-sensitive mechanisms, by optical chromatic aberrations (Flitcroft, 1989; Bradley *et al.*, 1992) or other means (see Discussion). Such effects might seriously compromise evidence for visual function at isoluminance (Livingstone & Hubel, 1987). While some studies have presented quite good evidence against the influence of such artifacts in the perception of motion at isoluminance, it often remains a matter of concern, particularly in view of the relative temporal delay between processing by long- and medium-wavelength sensitive cones (Walraven & Lee-Beck, 1964; deLange, 1958), which has recently been shown to mediate a motion percept (Stromeyer *et al.*, 1995). A powerful approach to this problem, which we adopt here, is to superimpose spatially and temporally broadband luminance noise over the chromatic stimuli, which masks the effects of any cross-activation of luminance detection mechanisms (Gegenfurtner & Kiper, 1992; Losada & Mullen, 1995).

A parallel processing of color and motion may be complicated by the existence of qualitatively distinct mechanisms mediating motion perception, proposed originally as "short-range" and "long-range" processes (Anstis, 1980; Braddick, 1980). The short-range process was thought to operate over small displacements and short periods of time, and to reflect properties of low-level mechanisms (Anstis, 1980; Braddick, 1980; Baker

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& Braddick, 1985). Operation of this process has been found to depend on the spatial frequency content of the stimulus (Chang & Julesz, 1983; Bischof & DiLollo, 1990; Cleary & Braddick, 1990; Boulton & Baker, 1991). The long-range process, exemplified by classical "phi" motion, was proposed to mediate apparent motion for larger displacements and longer time intervals, and to be characteristic of higher level processes.

More recently, a different formulation of two types of motion processing has been proposed (Chubb & Sperling, 1988; Cavanagh & Mather, 1989). A first-order (or Fourier) mechanism responds to directional components in the stimulus spatiotemporal Fourier power spectrum, and thus can be modelled by early linear spatiotemporal filters (Adelson & Bergen, 1985; van Santen & Sperling, 1985; Watson and Ahumada, 1985). A second-order (or non-Fourier) mechanism is proposed to mediate the perception of motion in stimuli whose movement is defined by variations of properties other than luminance, thus having no overall directional component in the Fourier power spectrum (Chubb & Sperling, 1988); motion of such stimuli must therefore involve a significant nonlinearity before the directional mechanism.

In a series of studies Boulton & Baker (1991, 1993a,b, 1994) have used random Gabor kinematograms to characterize two motion mechanisms. These stimuli consist of randomly placed Gabor function micropatterns, which are presented in two-flash apparent motion; motion is produced by a spatial displacement and a temporal separation between the two flashes. At relatively high micropattern densities and short time separations, the perceived direction of motion varies with displacement in a characteristically cyclic manner related to the carrier frequency of the Gabor micropatterns. This performance is dictated by the spatial frequency content of the stimulus elements, and can be explained by a quasi-linear mechanism (Boulton & Baker, 1993a). At low micropattern densities and/or longer time separations, however, motion can be seen for much larger displacements, with a limit determined by the density of micropatterns, but not by their internal structure (Boulton & Baker, 1993a); such performance can only be explained in terms of a directional mechanism whose inputs are nonlinear. The maximum displacement supporting motion,  $D_{\max}$ , shows abrupt discontinuities as a function of micropattern density (Boulton & Baker, 1993a) and as a function of temporal separation between flashes (Boulton & Baker, 1993b), emphasizing the categorically distinct nature of the underlying processes.

Thus, a single generic stimulus, the random Gabor kinematogram, can be used with differing stimulus parameters (high vs low-density, short vs long time separation) to characterize distinct motion mechanisms. The quasi-linear mechanism requires a similar micropattern orientation and spatial frequency on successive presentations, consistent with orientation- and spatial frequency-selective linear filtering; however, the nonlinear mechanism continues to provide good motion perception in spite of changes in micropattern carrier

across presentations (Boulton & Baker, 1994). Evidence from similar "limited-lifetime" Gabor apparent motion stimuli indicates that the nonlinear mechanism supports much higher velocities of motion than the quasi-linear mechanism, is less tolerant of added noise, and benefits more from the addition of multiple flashes (Baker & Hess, 1995).

Here, we further explore the differences between the two mechanisms, using random Gabor kinematograms composed of either red-green isoluminant micropatterns, or luminance-defined stimuli, both with superimposed luminance noise. Using high micropattern densities and short time separations to isolate the quasi-linear mechanism, we find a severe impairment of motion perception at isoluminance when cross-activation is masked. However, using low micropattern densities and longer time separations to isolate nonlinear motion mechanisms, motion perception remains robust for both isoluminant and isochromatic conditions.

## METHODS

The stimuli were generated with a PC-controlled frame-store (VSG2/2, Cambridge Research Systems) and displayed on a RGB monitor (Barco CCID 7751; Invar, Mk2) with a refresh rate of 125 Hz. The viewable portion of the screen had a spatial resolution of  $480 \times 441$  pixels, which subtended  $20.6 \times 15.2$  deg at a viewing distance of 100 cm. The z-nonlinearities of the red and green CRT guns were calibrated using a photometer (S-370, fitted with head No. 265, United Detector Technology), and the z-compensation was calculated using the inverse Gamma equations of Pelli & Zhang (1991); the blue gun was not used. The phosphors had CIE coordinates of ( $x = 0.623$ ,  $y = 0.341$ ) for the red, and ( $x = 0.278$ ,  $y = 0.584$ ) for the green, measured for this monitor by the National Research Council, Canada, using a Photo-Research PR-700\_PC Spectrascan. The stimulus mean luminance was  $6.5 \text{ cd/m}^2$ .

The stimulus consisted of two fields of pseudo-randomly positioned Gabor micropatterns, placed in horizontal strips centered  $5.0$  deg above and below a central fixation point (Boulton & Baker, 1991; Fig. 1). Presentation of the stimuli in the near periphery served to confine the stimulus in eccentricity (Baker & Braddick, 1985) and helped prevent observers from directing attention to the displacement of an individual micropattern fortuitously close to the fixation mark. Each micropattern was a small patch of a one-dimensional sinewave grating (carrier), enclosed in a smooth (gaussian) contrast envelope [Fig. 1(A)] producing a Gabor stimulus which was bandpass in both spatial frequency and orientation. Unless stated otherwise, the orientation of the sinewave carrier was vertical. The luminance-defined Gabor micropatterns had luminance distributions of the form:

$$L(x, y) = L_0 [1 + C \exp[-(x^2/2\sigma_x^2 + y^2/2\sigma_y^2)] \cdot \cos(2\pi x/\lambda)]$$

where  $L_0$  = mean luminance;  $C$  = contrast;  $\sigma_x$ ,  $\sigma_y$  = horizontal, vertical gaussian width parameters (here,

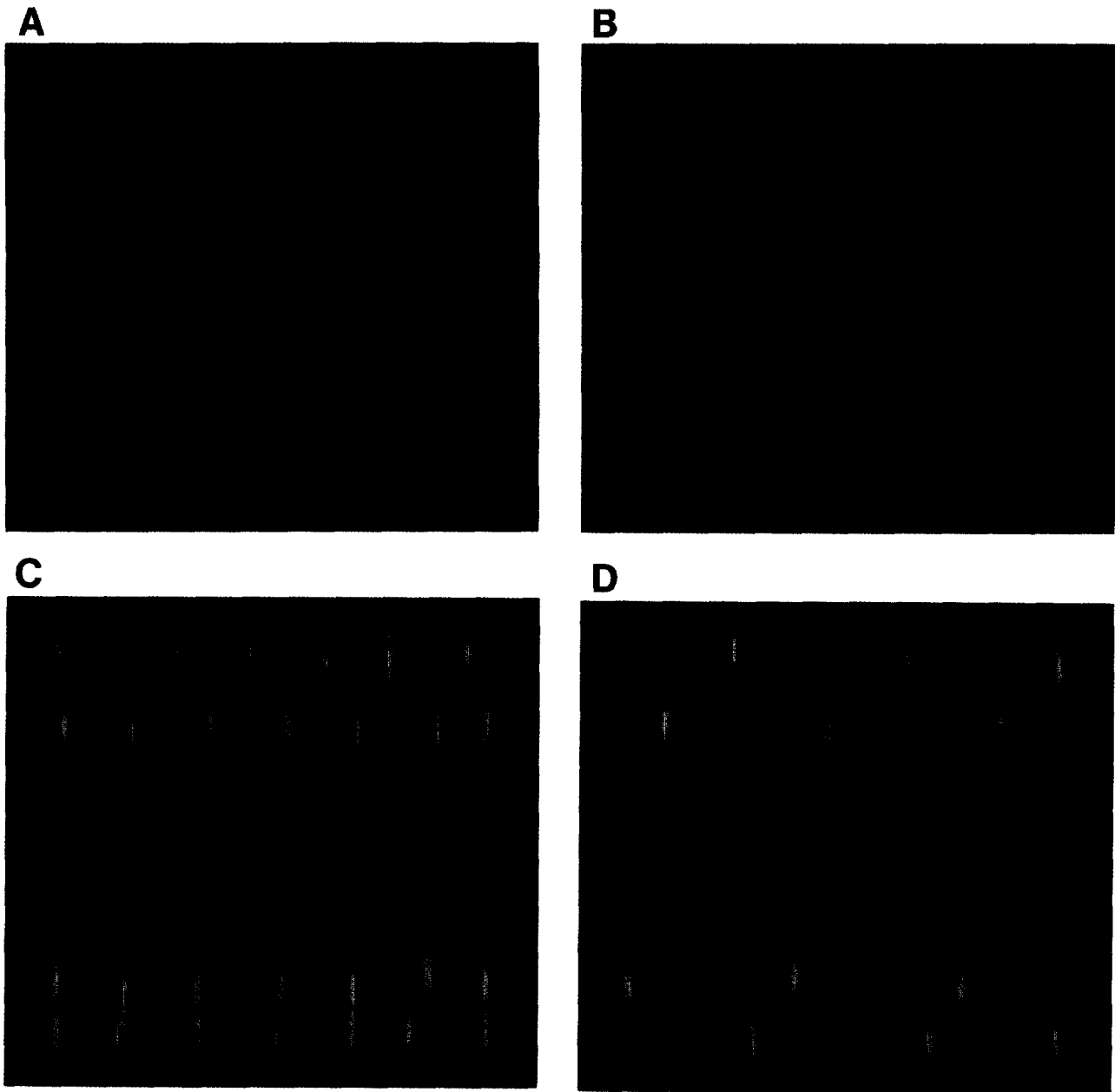


FIGURE 1. Spatial layout and parameters of stimuli. (A) A representative exposure of a two-flash random Gabor kinematogram, for a relatively high micropattern density (7 per row) used to isolate quasi-linear mechanism of motion detection. (B) Same as (A), but for a relatively low micropattern density (3 per row), used to isolate nonlinear mechanism of motion detection. For clarity, superimposed luminance noise is not shown. (C, D) Same as (A) and (B), respectively, but for luminance-defined stimuli.

always =  $3/4\lambda$ );  $\lambda$  = spatial wavelength of the cosine wave (1.0 deg).

Two-flash apparent motion was produced by presenting the field of micropatterns for a brief duration (100 msec), followed by displacement either to the left or right (with wrap-around at the display boundaries), with the same exposure duration. Any influence of eye movements was minimized by provision of a central fixation mark, off-foveal stimulus location, brief presentation times, and unpredictability of the direction of motion. The temporal separation between the onsets of the two exposures, the stimulus onset asynchrony (SOA), was either 100 or 150 msec. The same space-average

luminance and chromaticity was constant throughout the interstimulus and intertrial intervals.

Each trial was initiated by the observer, whose task was to report the direction of perceived motion (left or right) by a corresponding mouse button. A series of displacement values was tested in blocks of randomly interleaved trials, and performance was measured as the percentage errors (with at least 60 trials per displacement condition). Performance was measured for two conditions: for a high density of micropatterns [7 per stimulus row, Fig. 1(A)] with short SOA (100 msec) and for a low density of micropatterns [3 per row, Fig. 1(B)] with a long SOA (150 msec). These parameters were chosen on

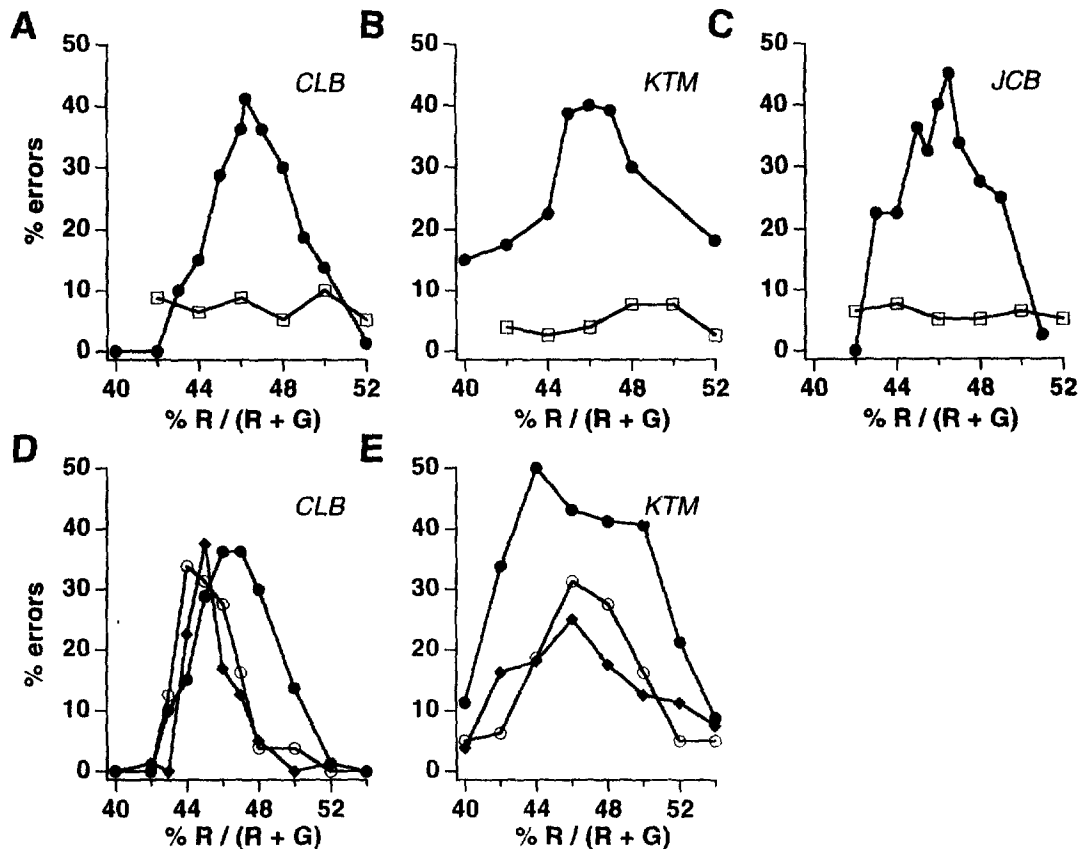


FIGURE 2. Procedure for determination of isoluminant points for each observer. (A) Percent errors in direction discrimination as a function of red/(red + green) ratio, at fixed jump sizes of  $\lambda/4$  (0.25 deg), for high-density/short SOA conditions (solid symbols) and  $3/2\lambda$  (1.5 deg), for low-density/long SOA conditions (open symbols). (B, C) Same as (A) for two other observers. Superimposed dynamic luminance noise was used throughout [(rms contrast of 4% in (A) and (C), 5.8% in (B))]. Note that performance deteriorates to near chance levels at a characteristic red/(red + green) value for high density/short SOA stimuli, while a good level of performance is maintained uniformly across red/(red + green) ratios for low-density/long SOA stimuli. (D) Same as (A), but only for high-density/short SOA stimuli, for three values of luminance noise (filled circles, 4%; open circles, 2%; diamonds, 0%). (E) Same as (D), for a second observer (filled circles, 5.8%; open circles, 2.85%; diamonds, 0%).

the basis of previous work (Boulton & Baker, 1993a,b) to isolate quasi-linear and nonlinear motion mechanisms, respectively, and were also confirmed in this experimental series with pilot measurements. Performance was measured for isoluminant stimuli (red–green) and also luminance stimuli (green–black) with the contrast of each equated to a defined logarithmic increment above each individual's detection threshold. Detection thresholds were measured in the presence of luminance noise as described below. All observers viewed the stimulus monocularly at a distance of 100 cm, and had normal or corrected-to-normal acuity.

The red–green isoluminant stimuli were generated by emulating a method used previously (Mullen, 1985). Look-up tables containing values forming a ramp were used for the red and green guns with opposite slopes (corrected for CRT  $z$ -nonlinearity). Chromatic stimuli were rendered as modulations of red/(red + green) luminance ratio about a yellow background of the space-averaged red–green ratio. The spatial frequency of 1 c/d was high enough to allow a sufficient number of micropatterns, but low enough to minimize any luminance artifact due to optical chromatic aberration (Bradley *et al.*, 1988; Flitcroft, 1989). This spatial

frequency is well within the contrast sensitivity passband of color vision (Mullen, 1985). Chromatic contrast was defined conventionally, as the Michelson contrast of the component red and green stimuli; a physical color contrast of 40% was used here, which was above the observers' detection threshold by 14–20 dB at the higher density, and by 11–18 dB at the lower density (see below).

All measurements, unless otherwise noted, were made in the presence of superimposed luminance noise. The noise had a uniform amplitude distribution and was spatially one-dimensional (vertical), dynamic, with a spatial and temporal frequency spectrum which was flat over the range determined by sizes of pixels and the display, and by the frame rate and presentation time. The noise amplitude was quantified as the square root of the noise energy,  $C_{rms}$ ; for the uniform noise amplitude distribution, this can easily be shown to be:

$$C_{rms} = C/\sqrt{3}$$

where  $C$  is the physical contrast. The luminance noise and chromatic stimuli were presented on alternate frames of the 125 Hz display, with synchronous alternation of look-up tables to produce red and green ramp slopes of

the same or of opposite sign, respectively. On each trial, the noise onset preceded the stimulus onset by 50 msec, and outlasted the end of the stimulus by 50 msec, to mask any temporally dynamical luminance signals such as might arise from differential L or M cone-based delays, typically in the order of 10–20 msec (Stromeyer *et al.*, 1995). This frame-wise interleaving of stimulus and noise acted to halve the effective contrasts of both; values of stimulus and noise contrast given here are compensated accordingly.

## RESULTS

The isoluminant point was determined separately for each observer by measuring direction discrimination for a Gabor kinematogram at a series of red/(red + green) ratios. Figure 2 shows results for direction discrimination performance as a function of red/(red + green) ratio. For Fig. 2(A, B and C) the filled circles show results for a stimulus that was spatially and temporally optimal for the quasi-linear mechanism: a short SOA (100 msec), a high density (7 micropatterns per row), and a displacement of  $\lambda/4$ . The open squares in Fig. 2(A, B and C) show direction discrimination performance under optimal conditions for the nonlinear mechanism: a sparse density (3 micropatterns per row), a long SOA (150 msec), and a

displacement of  $3/2\lambda$ . For observers CLB and JCB the stimulus had 4% luminance noise, and for observer KTM 5.8%. As can be seen, all three observers showed a degradation in performance, under conditions optimal for the quasi-linear mechanism, for a narrow range of red/green ratios. The red/green ratios used in the following experiments as the isoluminant points were determined from the peaks of these functions. Note the absence of any degradation in performance as a function of red–green ratio when stimulus parameters were optimal for the nonlinear mechanism [Fig. 2(A, B and C), square symbols].

The results in Fig. 2(D and E) show direction discrimination as a function of red–green ratio for different contrast levels of luminance noise, with the stimulus parameters optimal for the quasi-linear mechanism. For CLB [Fig. 2(D)] the filled circles show results with luminance noise rms contrast set at 4% rms contrast. The open circles show results for a luminance noise rms contrast of 2%, and the diamonds show results in the absence of noise: the latter two functions are skewed to the left, showing a relatively larger amount of green needed before performance collapsed. For KTM, performance at isoluminance deteriorated substantially for luminance noise contrasts of 2.85% (open circles) and

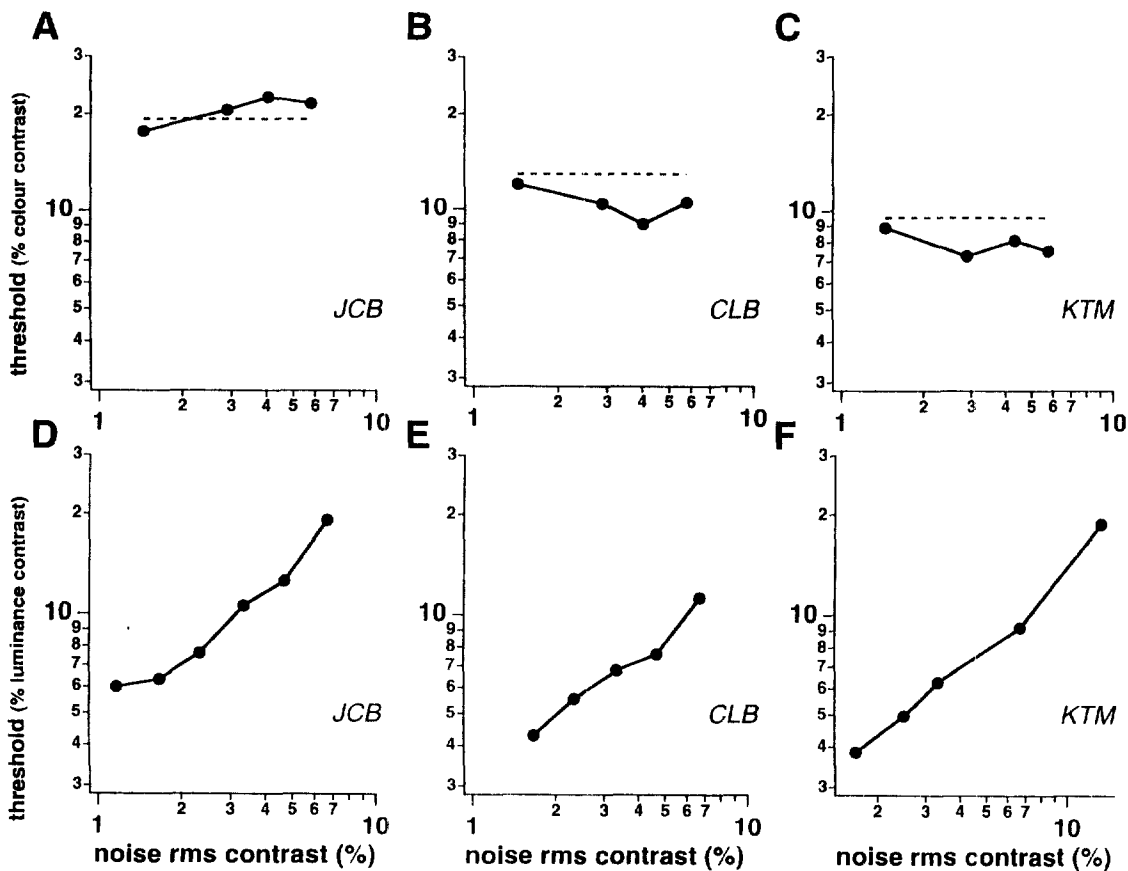


FIGURE 3. Effect of added luminance noise on detection thresholds for chromatic and luminance-defined random Gabor stimuli. (A) Color contrast threshold for detection of color Gabor kinematograms presented in apparent motion (low-density, large SOA, jump size  $3/2\lambda = 1.5$  deg). Dotted line indicates threshold in the absence of noise. (B, C) Same as (A), for two other observers, using high-density, short SOA, jump size  $\lambda/4$  (0.25 deg). (D, E, F) Same as (A, B, C) but for luminance-defined stimuli.

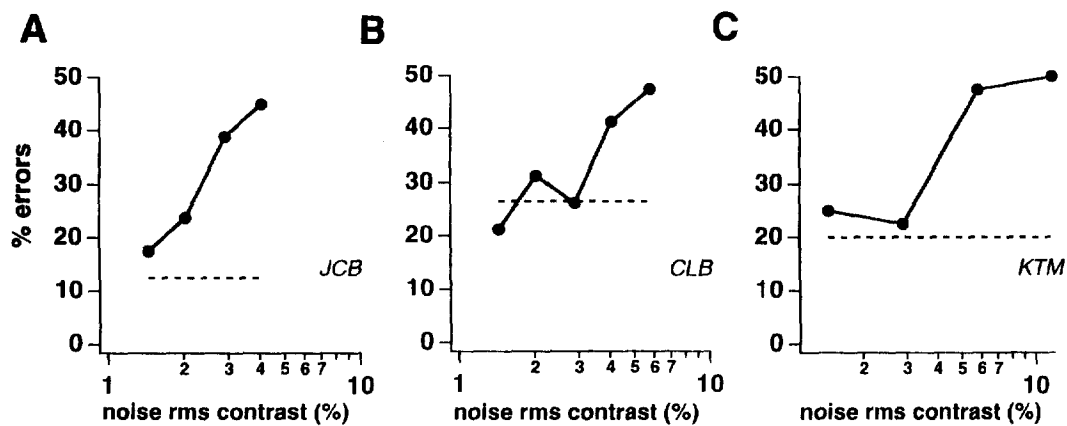


FIGURE 4. Effect of added luminance noise on direction discrimination. (A) Percent errors in direction discrimination, for high-density and short SOA random Gabor apparent motion, as a function of amount of added luminance noise. Effective chromatic contrast of 40%, at observer's isoluminant red/(red + green) ratio, as determined in Fig. 2. Dashed line indicates performance in the absence of noise. (B, C) Same as (A), for two other observers. These measurements show amount of luminance noise sufficient to mask residual luminance-mediated motion perception for high-density/short SOA stimuli.

0% (diamonds), and collapsed to near chance with 5.8% rms contrast luminance noise (filled circles).

To ensure that we were masking responses in the luminance mechanism and not the detection of the color stimulus itself, we measured thresholds for the detection of both high and low-density chromatic Gabor kinematograms (presented with a randomly varied direction of motion) in the presence of different levels of luminance noise [Fig. 3(A, B, C)]. A two-alternative spatial forced-choice procedure was used for the detection of the stimulus: on each trial the observer indicated whether a strip of the stimulus appeared in the upper or the lower position of the standard display. Psychometric functions of percentage errors against contrast were fit with Weibull functions (Weibull, 1951), and thresholds were taken at 18% errors. Thresholds were measured in the absence of noise, and in the presence of noise for a range of noise rms contrasts from 1.42 to 5.8% [Fig. 3(A, B, C)]. The dashed lines show detection thresholds in the absence of noise. Detection thresholds for the chromatic stimulus remained essentially constant with increasing luminance noise contrast, implying that luminance noise does not affect the mechanism used to detect the color stimulus (Gegenfurtner & Kiper, 1992; Losada & Mullen, 1995). Figure 3(D, E and F) show results for the same experiment for luminance stimuli. Here, detection threshold increased monotonically with noise contrast, with the implication that the noise and the luminance Gabor kinematogram are detected by a common mechanism (Burgess *et al.*, 1981). From these results we conclude that the luminance noise employed here is able to mask luminance signals without degrading the detection of the color stimulus, under the conditions of our motion experiments.

To ensure that any residual direction discrimination based on luminance artifacts was masked by the luminance noise, we also measured direction discrimination at isoluminance as a function of noise contrast. The red-green ratio that gave isoluminance was taken from the peak of the function presented in Fig. 2(A, B and C);

the other stimulus parameters were optimal for the quasi-linear mechanism (high-density, short SOA, displacement =  $\lambda/4$ ). The dashed lines in Fig. 4 indicate the performance measured in the absence of noise, for each of three observers. This performance, which was rather poor (but better than chance), rapidly degraded with increasing noise contrast, reaching chance levels with 4.0% contrast noise ( $C_{rms}$ ) for observers CLB and JCB, and 5.8% for KTM. The latter levels of luminance noise were used in all subsequent experiments.

Unless otherwise noted, chromatic stimuli were always presented at 40% chromatic contrast, which was 11–20 dB above detection threshold (depending on density and the observer). Luminance stimuli used for comparison were presented at luminance contrasts which were the same logarithmic increment above their detection thresholds, as the 40% chromatic gratings were above their detection thresholds, as measured in each observer. This matching of luminance and chromatic contrasts to be similarly above their detection thresholds was performed separately for the high-density/short SOA and the low-density/long SOA stimuli.

Previous studies using this type of stimulus (Boulton & Baker, 1993a,b) were replicated for micropatterns defined by luminance contrast. All stimuli were presented in the presence of luminance noise. The data in Fig. 5(A, B and C) (open squares) show that for a high micropattern density (7 micropatterns per stimulus row) and a short time interval between flashes (SOA = 100msec), direction discrimination performance depends on the displacement of the micropatterns relative to spatial periodicity of the carrier ( $\lambda$ ). Optimal performance is achieved for small displacements (around  $\lambda/4$ ), but larger displacements produce chance performance. For still larger displacement (around  $3/4\lambda$ ), motion is seen in the reverse direction (errors approaching 100%) before falling towards chance levels. This cyclic pattern of performance, whose periodicity corresponds to the wavelength ( $\lambda$ ) of the stimulus carrier frequency, is predicted by

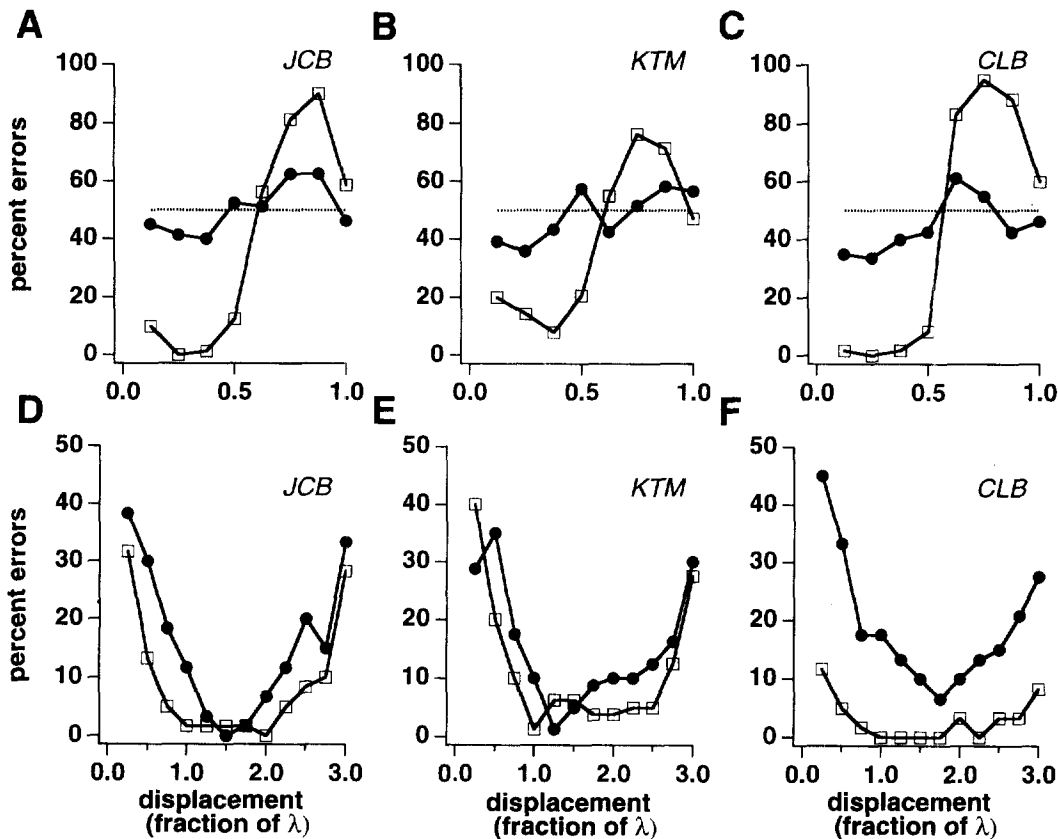


FIGURE 5. Psychometric functions for direction discrimination. (A, B, C) Percent errors as a function of jump size, for high-density/short SOA stimuli which isolate quasi-linear mechanism. Spatial wavelength,  $\lambda$ , of Gabor carrier was 24 pixels. Results with isoluminant stimuli shown by filled symbols, and luminance stimuli by open symbols. (D, E, F) Same as top row, but for low-density/long SOA stimuli which isolate a nonlinear mechanism. Luminance noise contrast 4% for JCB and CLB, 5.8% for KTM.

quasi-linear models of motion detection based on early linear spatiotemporal filters.\*

When a chromatic Gabor kinematogram with the same stimulus parameters and luminance noise is presented at isoluminance, we find that performance is near chance for the entire range of displacements tested [Fig. 5(A, B and C), filled circles]. Under these conditions the motion perception mediated by a quasi-linear mechanism is severely degraded at isoluminance, consistent with a conventional notion of the failure of chromatic motion processing.

Figure 5(D, E and F), (open squares) shows results for a low micropattern density (3 micropatterns per stimulus row) and longer time interval between flashes (SOA = 150 msec), with a luminance Gabor kinematogram. Good performance was obtained for a much larger range of displacements up to a limit determined by the

average spacing of micropattern envelopes along the path of motion, independent of the carrier frequency (Boulton & Baker, 1993a).† This good performance is maintained even for displacements (approx.  $3/4\lambda$ ) which elicit a reversal of perceived motion for the high-density and short SOA condition. This behavior is consistent with a nonlinear model, which discards the fine grain structure of the carrier and instead detects motion of the envelope.

Isoluminant color kinematograms in the low-density and large SOA condition also result in a good percept of motion. In these conditions direction discrimination performance [Fig. 5(D, E and F), filled circles] is remarkably similar in form (although slightly poorer) to that obtained for luminance stimuli. Good performance is obtained for a similar range of displacements with no evidence of the carrier-related cyclic dependence characteristic of a quasi-linear mechanism. Thus, color vision can detect motion via a nonlinear mechanism.

Is the mechanism that detects motion of isoluminant stimuli of the same nature as the nonlinear mechanism which detects movement of luminance stimuli? A simple kind of nonlinear motion mechanism which would exhibit this behavior would be a full-wave rectification followed by low-pass filtering of the image prior to extraction of the direction of motion (Chubb & Sperling, 1988). This would effectively remove the carrier

\*Formally this is "linear" behavior because the net directional energy of the Fourier power spectrum of the space-time stimulus is a good predictor of the cyclic psychometric function (Doshier *et al.*, 1989).

†The maximum displacement for the detection of motion ( $D_{max}$ ) is defined as a threshold on the first rise in the psychometric function towards chance.  $D_{max}$  is constant for micropattern densities above a critical value; below this critical density,  $D_{max}$  increases abruptly in magnitude, and is thereafter dependent (inversely) on the density of micropatterns in the stimulus (Boulton & Baker, 1993a).

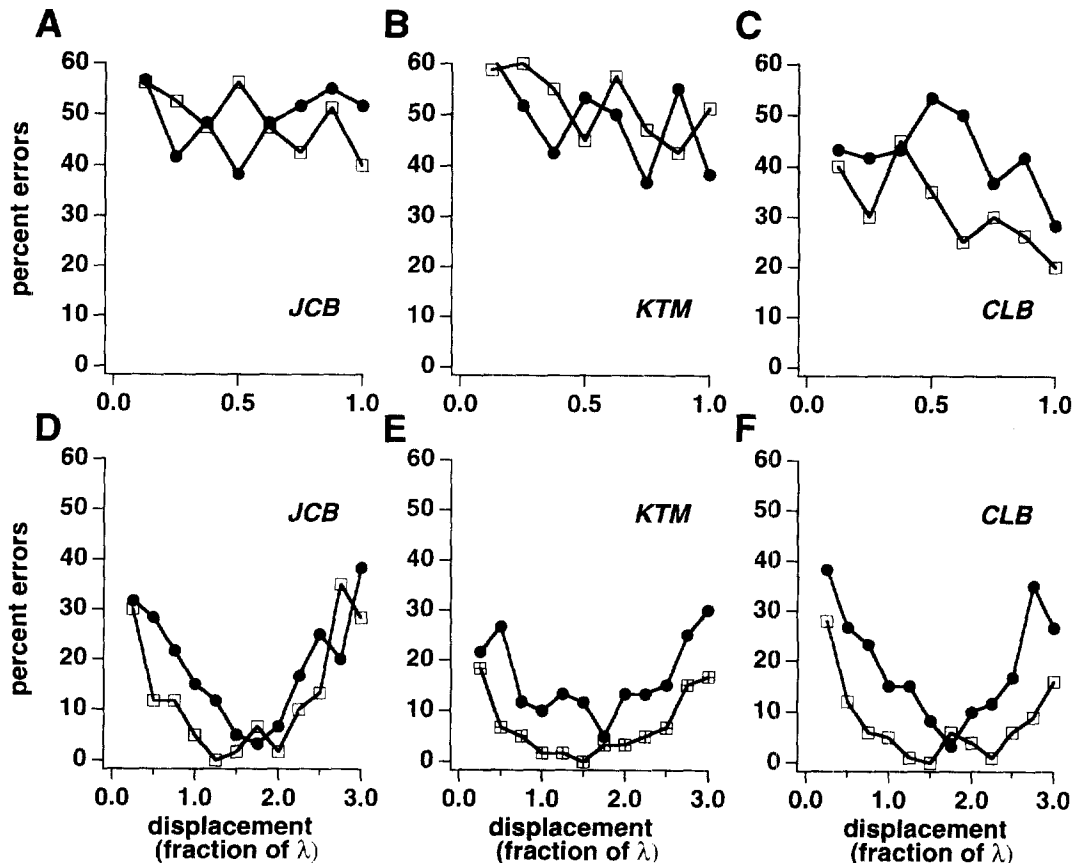


FIGURE 6. Effect of changing orientation of Gabor micropatterns across exposures. (A, B, C) For high-density/short SOA stimuli, good direction discrimination is abolished, both for isoluminant (filled symbols) and luminance (open symbols) stimuli. (D, E, F) Same as top row, but for low-density/long SOA stimuli, showing good performance of nonlinear mechanism for both isoluminant and luminance stimuli.

structure, leaving only the micropattern envelope. In such a scheme, the internal structure of the micropattern envelope could be changed between exposures of the motion sequence without disrupting the percept of motion. To test this kind of idea we presented the Gabor kinematogram with micropatterns having a vertical carrier on the first exposure and a horizontal carrier on the second exposure (Boulton & Baker, 1994). The task was once again direction discrimination, and the experiment was completed for four conditions: firstly, optimal parameters for the quasi-linear mechanism, presented with an isoluminant or an isochromatic stimulus, and secondly optimal parameters for the nonlinear mechanism, for isoluminant or isochromatic stimuli. All stimuli were presented at the same contrasts and luminance noise levels as previously.

Figure 6(A, B and C) show results for a high-density of Gabor micropatterns (7 per stimulus row) presented with a short SOA (100 msec), i.e., optimal parameters for the quasi-linear mechanism. Results show that motion perception is severely impaired under these conditions for both isoluminant stimuli (filled circles) and isochromatic stimuli (open squares). Performance did not show the cyclic function relative to the wavelength of the carrier frequency, as previously observed [Fig. 5(A, B and C), open squares] and was uniformly poor across all

displacements and conditions tested. This is expected if the mechanism is based on the output of spatially linear filters, with performance therefore related to the content of the micropatterns. Figure 6(D, E and F) shows results for changing orientation between exposures for a low density and long SOA, i.e. optimal parameters for the nonlinear mechanism. Good performance is obtained both for isoluminant and isochromatic stimuli (filled circles and open squares, respectively). If these data are compared with those in Fig. 5(D, E and F) there is little difference in performance for either the isoluminant or the isochromatic stimuli. That is, for both color and luminance, the nonlinear-mediated motion is not disrupted by a change in orientation of 90 deg between the exposures of the motion sequence. This supports the idea that the nonlinear mechanism responsible for motion detection by color vision is the same as that revealed with luminance stimuli.

Since the nonlinear mechanism is able to process both luminance and chromatic stimuli, we wondered whether it could integrate the two across successive exposures within a single presentation of two-flash apparent motion. To investigate this we presented a motion sequence whereby the first exposure comprised isoluminant micropatterns, and the second exposure isochromatic micropatterns. Red/green micropatterns on a yellow background were used in



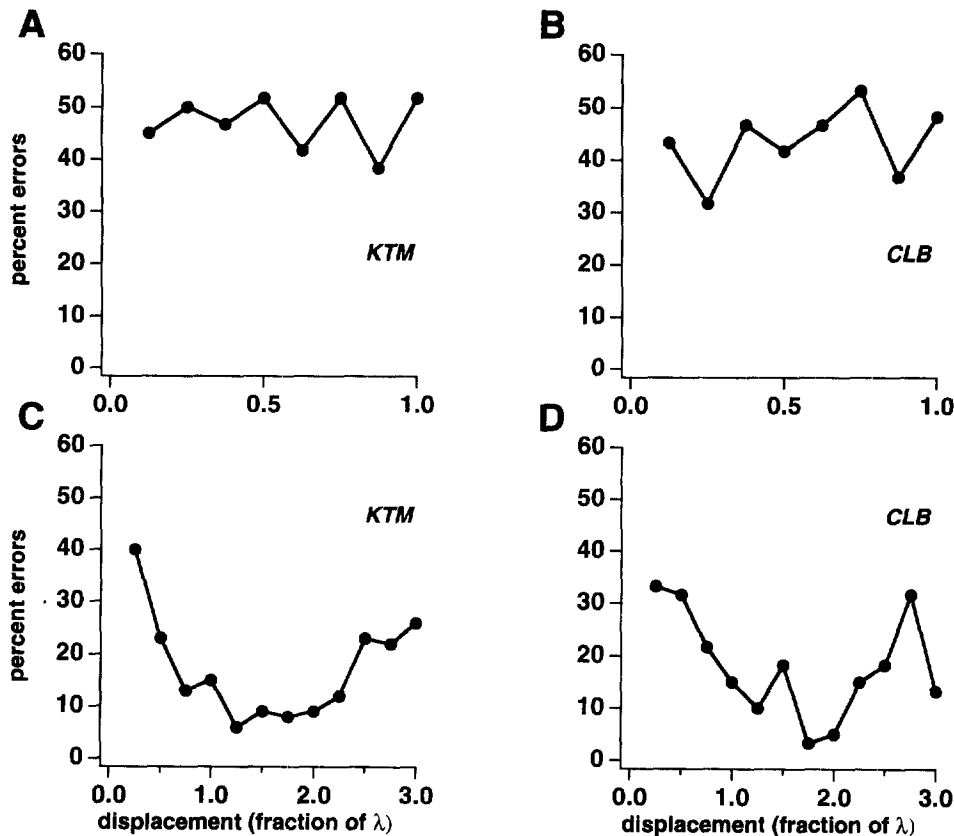


FIGURE 7. Effect of changing from color to luminance across exposures. First flash was red-green isoluminant, second flash was yellow-black luminance-defined. (A, B) For high-density/short SOA stimuli, quasi-linear motion fails. (C, D) For low-density/long SOA stimuli, nonlinear motion is able to integrate across chromatic and luminance inputs.

the first exposure and bright/dark yellow micropatterns on the same yellow background in the second exposure. The spatial frequency and orientation content of the micropatterns was unchanged between exposures. The same levels of luminance noise and micropattern contrasts were used as previously. This "color to luminance" motion sequence was presented first under conditions optimal for the quasi-linear mechanism (high-density, short SOA), and second under conditions optimal for the nonlinear mechanism (low-density, large SOA).

Figure 7(A and B) show results for the "color to luminance" stimulus presented with parameters suitable for the quasi-linear mechanism. Performance is around chance level, i.e., the mechanism fails under these conditions. This is consistent with results shown in Fig. 5(A, B and C), in which the quasi-linear mechanism is severely degraded at isoluminance, whereas performance is very good for luminance stimuli with the same spatial and temporal parameters. Figure 7(C and D), however, show that under conditions suitable for the nonlinear mechanism, good performance is obtained across a broad range of displacements characteristic of the nonlinear motion mechanism [compare Fig. 5(E and F), Fig. 6(E and F) with Fig. 7(C and D)]. These results indicate that the nonlinear mechanism can indiscriminately pool

luminance and chromatic signals, prior to the determination of direction of motion.

## DISCUSSION

Our results demonstrate that, in the presence of a dynamic luminance noise mask, random kinematograms using a high density of Gabor micropatterns and a short stimulus onset asynchrony can elicit motion perception for luminance-defined stimuli, which is greatly impaired for isoluminant chromatic stimuli. This indicates that the previously described "quasi-linear" mechanism of apparent motion (Boulton & Baker, 1993a,b, 1994) is driven principally or perhaps entirely by achromatic signals, consistent with early ideas of a separation between motion and color processing. However, we also show that the same stimulus with a low density of micropatterns and a longer SOA can provide good motion perception when it is isoluminant as well as isochromatic; this performance is maintained at much larger displacements than the size of the Gabor micropatterns, and despite changing orientation between flashes, indicating a nonlinear mechanism of apparent motion which is competent to handle chromatic as well as luminance inputs. If these results apply to more general kinds of motion perception, they suggest that when motion is seen at isoluminance, it is detected by a nonlinear (second-order, or non-Fourier) motion mechanism.\*

\*In this regard it seems unwise to use the term "first-order" to refer to stimuli whose motion attributes are defined by variations in color.

### *The role of cross-activation of luminance mechanisms*

A nominally isoluminant color stimulus at suprathreshold chromatic contrast might mediate the percept of motion by inadvertently cross-activating a luminance mechanism. Such "luminance cross-activation" can arise from optical chromatic aberrations, which are especially likely with the use of spatially sharp-edged stimuli. Our spatially narrowband stimuli, centered at 1 cpd, should largely avoid this problem (Flitcroft, 1989; Bradley *et al.*, 1992). Luminance cross-activation might also arise from neural factors such as the inhomogeneity of isoluminant points in LGN neurons (Derrington *et al.*, 1984) or second harmonic responses in M-cells to chromatic gratings (Lee *et al.*, 1990; see Dobkins & Albright, 1993, 1994).

Another potential source of luminance cross-activation may arise from the relative temporal delay between L- and M-type cones (deLange, 1958; Walraven & Lee-Beck, 1964; Stromeyer *et al.*, 1994, 1995). The latter authors demonstrate that L-cones can lag M-cones by about 16 msec at 4–9 Hz. This temporal phase shift can produce a luminance signal from nominally isoluminant drifting or flickering gratings, which can carry a percept of motion (Stromeyer *et al.*, 1995); it would presumably also produce a transient luminance signal at the onset and offset of the spatial chromatic borders of flashed stimuli, such as those used in apparent motion. During pilot experiments, without the use of luminance masking noise, we found good direction discrimination using nominally isoluminant kinematograms optimal for quasi-linear motion, at small values of ISI (less than about 20 msec), as might be expected from small differential latencies between the L and M cone signals. The addition of luminance noise eliminated the residual chromatic motion (Fig. 4) found in the pilot experiments, further supporting the idea that it was based on luminance cross-activation. Our nonlinear chromatic motion is unlikely to involve signals from such relative delays of cone mechanisms because of the large ISI (50 msec). Our strongest evidence against any kind of luminance cross-activation for nonlinear motion is its robust survival in the presence of added luminance noise, which is sufficient to severely impair the quasi-linear motion.

### *Comparison with other studies*

The failure of chromatic quasi-linear motion agrees with the many studies which support conventional ideas of motion failure at isoluminance (e.g., Ramachandran & Gregory, 1978; Palmer *et al.*, 1993), and suggests that those studies used stimuli and tasks which depended primarily on the quasi-linear motion mechanism. On the other hand, our finding of nonlinear chromatic motion may support previous reports of chromatic motion: motion aftereffects from drifting isoluminant gratings (Wohlgemuth, 1911; Cavanagh & Favreau, 1985; Derrington & Badcock, 1985; Mullen & Baker, 1985), apparent motion from isoluminant random dot kinematograms (Cavanagh *et al.*, 1985), slowing of perceived speed by addition of color (Cavanagh *et al.*, 1984), and

"smooth" rather than "jerky" motion of drifting isoluminant gratings at higher color contrasts (Mullen & Boulton, 1992). Some of these findings might have been due to luminance cross-activation, but others may have used stimuli and/or tasks which depended primarily on a nonlinear motion mechanism. In some cases such a correspondence would imply that the nonlinear mechanism can detect the motion of drifting sinewave gratings, notwithstanding their being conventionally deemed "first-order" stimuli. This idea might be consistent with the results of Cropper & Derrington (1994), who found that direction discrimination of drifting chromatic gratings had a duration dependence like that of non-Fourier stimuli (beats) at low color contrast, and like that of luminance gratings at high color contrasts (perhaps via luminance cross-activation).

Dobkins & Albright (1993, 1994) employed multi-flash apparent motion of chromatic sinewave gratings, which reversed chromatic contrast on successive displacements; a "signed" motion correspondence mechanism (which preserves the chromatic labels of spatial regions) would show a reversal of perceived direction of motion, while an "unsigned" mechanism (responding to chromatic borders, regardless of polarity) would not. Both human psychophysics (Dobkins & Albright, 1993) and single unit recordings in primate area MT/V5 (Dobkins & Albright, 1994) indicated an unsigned mechanism at small displacements ( $0.07\lambda$  and below), and a signed mechanism for larger displacements ( $0.14$ – $0.25\lambda$ ).

Psychophysical studies of apparent motion using non-isoluminant stimuli which change either luminance or color on successive exposures (Papathomas *et al.*, 1991; Gorea *et al.*, 1993; Morgan & Ingle, 1994) have also argued for a "signed" chromatic motion mechanism. However, the results of adding luminance noise to such stimuli (Gorea *et al.*, 1993) are suggestive of a role of luminance cross-activation. More convincing evidence for signed chromatic motion was provided by Cropper & Derrington (1996), who showed motion perception for chromatic displaced sinewave gratings, in spite of superimposed (albeit stationary) luminance maskers.

In our experiments a "signed" chromatic motion mechanism should produce psychometric functions periodic with the Gabor carrier wavelength, i.e., quasi-linear motion. Our data provide almost no indication of a signed chromatic motion mechanism when luminance noise is added. The above studies differed from ours in one or more ways: foveal rather than eccentric presentation, multi-flash instead of two-flash sequences, very different temporal conditions, the use of sharp-edged stimuli, and/or the setting of luminance levels by flicker photometry or by instrumental measurement rather than with the task itself. It would be interesting to repeat some of these experiments with spatially bandlimited stimuli and added dynamic luminance noise, to circumvent complications from luminance cross-activation. Our results do not preclude a linear chromatic motion mechanism that might be revealed using other stimuli

or tasks, but they indicate that if a truly chromatic “signed”/quasi-linear motion signal exists, it is evidently very much weaker than the unsigned/nonlinear one revealed here.

#### *Physiological substrates of two mechanisms for motion detection*

Some characteristics of our quasi-linear and nonlinear motion mechanisms are suggestive of mediation by the magnocellular and parvocellular pathways, respectively. The failure of quasi-linear motion at isoluminance, its steep dependence on contrast (Boulton & Baker, 1994) and its tuning to relatively short SOAs seem comparable to the high contrast gain and faster temporal dynamics of M-cells. Conversely, the nonlinear motion’s operation at isoluminance (even in the presence of luminance masking), shallow dependence on contrast, and preference for longer time intervals are suggestive of mediation by P-cells.

An alternative level of comparison is in terms of luminance vs chromatic mechanisms which are inferred from psychophysical experiments; these channels carry (L + M) and (L – M) cone signals, respectively, which behave as separable (independent) mechanisms, based on the shape of threshold contours (Cole *et al.*, 1993; Sankeralli & Mullen, 1996; Metha *et al.*, 1994), subthreshold summation (Mullen *et al.*, 1997), adaptation (Bradley *et al.*, 1988; Krauskopf *et al.*, 1982), and noise masking (Gegenfurtner & Kiper, 1992; Losada & Mullen, 1995). The quasi-linear mechanism’s impairment at isoluminance and vulnerability to luminance noise indicate that it is driven by a luminance mechanism; such a luminance mechanism might well receive both magno- and parvocellular inputs, which carry motion over complementary spatial and temporal frequency ranges (Schiller & Logothetis, 1990; Merigan *et al.*, 1991). Since our nonlinear chromatic motion is robust against luminance noise, it can be carried by a true chromatic (color-opponent) mechanism; on the other hand, its competence to handle luminance-defined stimuli indicates it can also accept luminance mechanism signals. A physiological substrate of orthogonal chromatic and luminance mechanisms is not yet established; it is clearly not LGN M- vs P-cells, since the P-cells are univariant for color and luminance contrast at most spatial frequencies (Derrington *et al.*, 1984).

These findings further strengthen the evidence for a dichotomy between quasi-linear and nonlinear mechanisms in apparent motion (Boulton & Baker, 1993a,b, 1994), particularly reinforcing the pattern of findings in which the nonlinear mechanism is much more indiscriminate in stimulus requirements. Quasi-linear motion operates only for small displacements (relative to the stimulus bandwidth), requires nearly identical spatial frequency and orientation across exposures, and is severely impaired at isoluminance. The nonlinear mechanism, however, carries motion for much larger displacements, is able to integrate across flashes whose Gabor micropatterns differ in orientation (Fig. 6) or in

spatial frequency, and is operative for isoluminant, isochromatic, and mixed “color to luminance” stimuli (Fig. 7). Thus, the nonlinear motion mechanism could be functionally significant as a means of greatly extending the range of conditions under which motion can be detected beyond those handled by the narrowly tuned quasi-linear mechanism, at the expense of a greater probability of erroneous responses in noisy or cluttered conditions.

## 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.
- Anstis, S. (1980). The perception of apparent motion. *Philosophical Transactions of the Royal Society of London B*, 290, 153–168.
- Baker, C. L. Jr. & Braddick, O. J. (1985). Eccentricity dependent scaling of the limits for short range apparent motion perception. *Vision Research*, 25, 803–812.
- Baker, C. L. Jr. & Hess, R. F. (1995). Limited-lifetime random Gabor stimuli reveal two underlying motion mechanisms. *Investigative Ophthalmology and Visual Science*, 36, S395.
- Bischof, W. F. & DiLollo, V. (1990). Perception of directional sampled motion in relation to displacement and spatial frequency: evidence for a unitary system. *Vision Research*, 30, 1341–1362.
- Boulton, J. & Baker, C. L. Jr. (1991). Motion detection is dependent on spatial frequency not size. *Vision Research*, 31, 77–87.
- Boulton, J. & Baker, C. L. Jr. (1993a). Different parameters control motion perception above and below a critical density. *Vision Research*, 33, 1803–1811.
- Boulton, J. & Baker, C. L. Jr. (1993b). Dependence on stimulus onset asynchrony in apparent motion: evidence for two mechanisms. *Vision Research*, 33, 2013–2019.
- Boulton, J. & Baker, C. L. Jr. (1994). Psychophysical evidence for both a “quasi-linear” and a “nonlinear” mechanism for the detection of motion. In Lawton, T. B. (Ed), *Computational vision based on neurobiology* (pp. 124–133). S.P.I.E. Proc., Vol. 2054.
- Braddick, O. J. (1980). Low-level and high-level processing in apparent motion. *Philosophical Transactions of the Royal Society of London B*, 290, 137–151.
- Bradley, A., Switkes, E. & DeValois, K. (1988). Orientation and spatial frequency selectivity of adaptation to color and luminance gratings. *Vision Research*, 28, 841–856.
- Bradley, A., Zhang, L. & Thibos, L. N. (1992). Failures of isoluminance caused by ocular chromatic aberration. *Applied Optics*, 31, 3657–3667.
- Burgess, A. E., Wagner, R. F., Jennings, R. J. & Barlow, H. B. (1981). Efficiency of human visual detection. *Science*, 214, 93–94.
- Cavanagh, P. & Anstis, S. (1991). The contribution of color to motion in normal and color-deficient observers. *Vision Research*, 31, 2109–2148.
- Cavanagh, P., Boeglin, J. & Favreau, O. E. (1985). Perception of equiluminous kinematograms. *Perception*, 14, 151–162.
- Cavanagh, P. & Favreau, O. E. (1985). Color and luminance share a common motion pathway. *Vision Research*, 25, 1595–1601.
- Cavanagh, P. & Mather, G. (1989). Motion: the long and the short of it. *Spatial Vision*, 4, 103–129.
- Cavanagh, P., Tyler, C. W. & Favreau, O. (1984). Perceived velocity of moving chromatic gratings. *Journal of the Optical Society of America*, 1, 893–899.
- Chang, J. J. & Julesz, B. (1983). Displacement limits for spatial frequency filtered random-dot cinematograms in apparent motion. *Vision Research*, 23, 1379–1385.
- Chichilnisky, E. J., Heeger, D. & Wandell, B. A. (1993). Functional segregation of color and motion perception examined in motion nulling. *Vision Research*, 33, 2113–2125.
- Chubb, C. & Sperling, G. (1988). Drift-balanced random stimuli: A

- general basis for studying non-Fourier motion perception. *Journal of the Optical Society of America A*, 5, 1986–2006.
- Cleary, R. & Braddick, O. J. (1990). Direction discrimination for bandpass filtered random dot kinematograms. *Vision Research*, 30, 303–316.
- Cole, G. R., Hine, T. & McIlhagga, W. (1993). Detection mechanisms in l-, m-, and s-cone contrast space. *Journal of the Optical Society of America*, 10, 38–51.
- 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.
- deLange, H. (1958). Research into the dynamic nature of the human fovea-cortex systems with intermittent and modulated light. II. Phase shift in brightness and delay in color perception. *Journal of the Optical Society of America*, 48, 784–789.
- 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., Krauskopf, J. & Lennie, P. (1984). Chromatic mechanisms in LGN of macaque. *Journal of Physiology*, 357, 241–265.
- DeYoe, E. A. & van Essen, D. C. (1988). Concurrent processing streams in monkey visual cortex. *Trends in Neuroscience*, 5, 219–226.
- 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.
- Dosher, B. A., Landy, M. S. & Sperling, G. (1989). Kinetic depth effect and optic flow—I. 3D shape from Fourier motion. *Vision Research*, 29, 1789–1813.
- Flitcroft, D. I. (1989). The interactions between chromatic aberration, defocus and stimulus chromaticity: implications for visual physiology and colorimetry. *Vision Research*, 29, 349–360.
- Gegenfurtner, K. R. & Kiper, D. C. (1992). Contrast detection in luminance and chromatic noise. *Journal of the Optical Society of America*, 9, 1880–1888.
- 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.
- Hubel, D. H. & Livingstone, M. S. (1987). Segregation of form, color and stereopsis in primate area 18. *Journal of Neuroscience*, 7, 3378–3415.
- Krauskopf, J., Williams, D. R. & Heeley, D. W. (1982). Cardinal directions of color space. *Vision Research*, 22, 1123–1131.
- 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*, 7, 2223–2236.
- Livingstone, M. S. & Hubel, D. H. (1987). Psychophysical 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*, 12, 250–260.
- 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., Vingrys, A. J. & Badcock, D. R. (1994). Detection and discrimination of 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 a signed-colour input to motion detection. *Vision Research*, 34, 2527–2535.
- Mullen, K. T. (1985). The contrast sensitivity of human color vision to red-green and blue-yellow chromatic gratings. *Journal of Physiology*, 359, 381–400.
- Mullen, K. T. & Baker, C. L. Jr. (1985). A motion aftereffect from an isoluminant stimulus. *Vision Research*, 25, 685–688.
- Mullen, K. T. & Boulton, J. (1992). Absence of smooth motion perception in color vision. *Vision Research*, 32, 483–488.
- Mullen, K. T., Cropper, S. J. & Losada, M. A. (1997). Absence of linear subthreshold summation between red-green and luminance mechanisms over a wide range of spatiotemporal conditions. *Vision Research*, 37, 1157–1165.
- 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, 1883–1892.
- Pelli, D. & Zhang, L. (1991). Accurate control of contrast on microcomputer displays. *Vision Research*, 31, 1337–1350.
- Ramachandran, V. S. & Gregory, R. L. (1978). Does colour provide an input to human motion perception? *Nature*, 275, 55–56.
- Sankeralli, M. & Mullen, K. T. (1996). Estimation of the L-, M-, and S-cone weights of the post-receptoral detection mechanisms. *Journal of the Optical Society of America*, 13, 909–915.
- Schiller, P. H. & Logothetis, N. K. (1990). The color-opponent and broad-band channels of the primate visual system. *Trends in Neurosciences*, 13, 392–398.
- Stromeyer, C. F. III, Chaparro, A., Tolia, A. S. & Kronauer, R. E. (1994). Colored fields produce large L vs M phase shifts in luminance motion mechanism. *Investigative Ophthalmology and Visual Science*, 35, 1644.
- Stromeyer, C. F. III, Kronauer, R. E., Ryu, A., Chaparro, A. & Eskew, R. T. Jr (1995). Contributions of human long-wave and middle-wave cones to motion detection. *Journal of Physiology*, 485, 221–243.
- Ungerleider, L. G. & Mishkin, M. (1982). Two cortical visual streams. In Ingle, D. J., Goodale, M. A. & Mansfield, R. J. W. (Eds), *Analysis of visual behaviour* (pp. 549–586). Cambridge, MA: MIT Press.
- van Essen, D. C. & Maunsell, J. H. R. (1983). Hierarchical organization and functional streams in the visual cortex. *Trends in Neuroscience*, 6, 370–375.
- van Santen, J. P. H. & Sperling, G. (1985). Elaborated Reichardt detectors. *Journal of the Optical Society of America A*, 2, 300–321.
- Walraven, P. L. & LeeBeck, H. J. (1964). Phase shift of sinusoidally alternating colored stimuli. *Journal of the Optical Society of America*, 54, 78–82.
- Watson, A. B. & Ahumada, A. J. Jr (1985). Model of human visual motion sensing. *Journal of the Optical Society of America A*, 1, 322–342.
- Weibull, W. A. (1951). A statistical distribution function of wide applicability. *Journal of Applied Mechanics*, 18, 292–297.
- Wohlgemuth, A. (1911). On the after-effect of seen movement. *Br. J. Psychol. Monogr. Suppl.* 1.
- Zeki, S. M. (1978). Functional specialization in the visual cortex of the rhesus monkey. *Nature*, 274, 423–428.

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