S-cone contributions to linear and non-linear motion processing

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Abstract

We investigated the characteristics of mechanisms mediating motion discrimination of S-cone isolating stimuli and found a double dissociation between the effects of luminance noise, which masks linear but not non-linear motion, and chromatic noise, which masks non-linear but not linear motion. We conclude that S-cones contribute to motion via two different pathways: a non-linear motion mechanism via a chromatic pathway and a linear motion mechanism via a luminance pathway. Additionally, motion discrimination and detection thresholds for drifting, S-cone isolating Gabors are unaffected by luminance noise, indicating that grating motion is mediated via chromatic mechanisms and based on higher-order motion processing.
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1. Introduction

The detection of motion for purely color-defined stimuli has been a topic of much interest for some time, with the debate being mainly focussed on whether the human visual system is able to discriminate the motion of stimuli modulated along the isoluminant red–green (L/M-cone opponent) axis. There has been much evidence to suggest that we are unable to discriminate the motion of isoluminant red–green (RG) stimuli that are solely defined by L/M-cone modulations under certain conditions, including those of two-flash apparent motion stimuli (Bilodeau & Faubert, 1999; Ramachandran & Gregory, 1978), isoluminant grating stimuli near detection threshold (Cavanagh & Anstis, 1991; Hawken, Gegenfurtner, & Tang, 1994; Lindsey & Teller, 1990; Metha & Mullen, 1998; Mullen & Boulton, 1992a), and isoluminant grating stimuli masked by luminance noise (Mullen, Yoshizawa, & Baker, 2003).

On the other hand, studies have also shown that the loss of RG chromatic motion is not complete, since at isoluminance above detection threshold, the motion of red–green

gratings can be discriminated, although it appears slower than that of their luminance counterparts (Cavanagh, Tyler, & Favreau, 1984; Livingstone & Hubel, 1987; Lu, Lesmes, & Sperling, 1999; Mullen & Boulton, 1992a). Based on this gap between the motion and simple detection thresholds of isoluminant red–green chromatic stimuli, it has been suggested that motion and simple detection are mediated by different mechanisms (Derrington & Henning, 1993; Lee & Stromeyer, 1989; Lindsey & Teller, 1990; Metha, Vingrys, & Badcock, 1994; Mullen & Boulton, 1992a; Palmer, Mobley, & Teller, 1993; Stromeyer, Kronauer, Ryu, Chaparro, & Eskew, 1995), with the gap between motion and detection thresholds for RG isoluminant extending over a wide range of temporal frequencies (Metha & Mullen, 1998). Further evidence for a color contribution to motion comes from the observation that a motion after effect can be obtained from isoluminant chromatic stimuli (Cavanagh & Favreau, 1985; Derrington & Badcock, 1985; Mullen & Baker, 1985). Moreover, there is also evidence for interactions between color and luminance contrast in the perceived velocity of motion of gratings under some conditions (Cavanagh et al., 1984; Mullen & Boulton, 1992b) indicating that color plays a role in motion processing.

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Some of these seemingly contradictory findings on the ability of color vision to support motion perception may be rationalized by recognizing there are two fundamentally distinct types of mechanism mediating motion discrimination, one which is sensitive to first-order (linear) and another sensitive to higher-order (non-linear) spatial variations (Baker, Boulton, & Mullen, 1998; Baker & Hess, 1998; Boulton & Baker, 1993a, 1993b; Cavanagh & Mather, 1989; Julesz, 1981). For color vision, it has been demonstrated that red–green chromatic mechanisms per se do not support linear motion and that mechanisms mediating linear motion of nominally isoluminant red–green chromatic stimuli are luminance based (Lu et al., 1999; Yoshizawa, Mullen, & Baker, 2000), for a review of this topic see Cropper and Wuerger (2005). On the other hand, it has been demonstrated that red–green color vision can indeed support motion discrimination when mediated by higher-order or non-linear motion mechanisms (Cropper & Derrington, 1994; Derrington & Henning, 1993; Lu et al., 1999; Lu & Sperling, 1996; Lu & Sperling, 2001; Yoshizawa et al., 2000).

It is clear that in order to elucidate the issue of whether color plays a part in motion processing, a thorough analysis requires that a distinction be made between linear and non-linear motion. Previous studies have demonstrated that Gabor micropatterns presented in two-frame apparent motion, with a high density of micropatterns and short inter-stimulus duration will stimulate a linear motion mechanism. Conversely, non-linear motion mechanisms are stimulated with a low density of micropatterns and a long inter-stimulus duration (Baker et al., 1998; Baker & Hess, 1998; Boulton & Baker, 1993a, 1993b; Clifford, Freedman, & Vaina, 1998; Yoshizawa et al., 2000).

The analysis of color vision's contribution to linear and non-linear motion mechanisms has so far been limited to the L/M-cone opponent mechanisms (Mullen et al., 2003). The role of S-cones in motion discrimination, however, is still unclear. Some studies have indicated that S-cones alone are not effective at motion processing (Cavanagh et al., 1984; Ruppertsberg, Wuerger, & Bertamini, 2003), or that motion may be mediated by an S-cone input to the luminance pathway (Lee & Stromeyer, 1989). Other evidence suggests there may be a small S-cone input to motion processing (Cavanagh & Anstis, 1991; Dougherty, Press, & Wandell, 1999; Gegenfurtner & Hawken, 1995) and a more recent study indicates that some form of global motion processing is available to S-cones (Ruppertsberg, Wuerger, & Bertamini, 2006), but this has a strong dependence on the choice of stimulus parameters. The role of S-cones in discriminating linear versus non-linear motion has not been previously investigated.

In the present study, we examined motion discrimination for S-cone modulated stimuli and demonstrate that S-cones can mediate chromatic motion discrimination under specific conditions. We used a two-flash apparent motion paradigm, with stimuli that stimulate either linear or non-linear motion mechanisms, to determine the nature of motion detection and discrimination for S-cones. Additionally, for comparison with previous literature, we investigated thresholds for detection and direction discrimination of smoothly drifting, S-cone isolating Gabor stimuli.

2. Methods

2.1. Apparatus

For the majority of the experiments (Figs. 1–8), stimuli were presented to subjects on a Mitsubishi Diamond Pro 2070SB RGB monitor driven using a graphics card (VSG2/5, Cambridge Research Systems), which provides a contrast resolution of 14 bits. The frame rate of the monitor was 120 Hz non-interlaced and the spatial resolution of the screen was 1024×769 pixels. The stimuli were viewed in a darkened room and the mean luminance of the monitor was 50 cd/m^2. For the data in Fig. 9, a
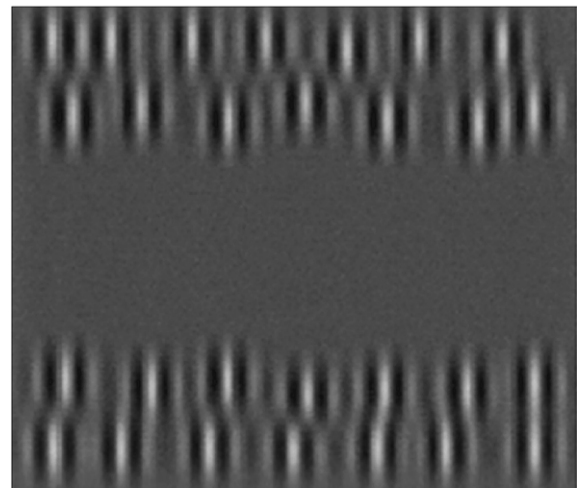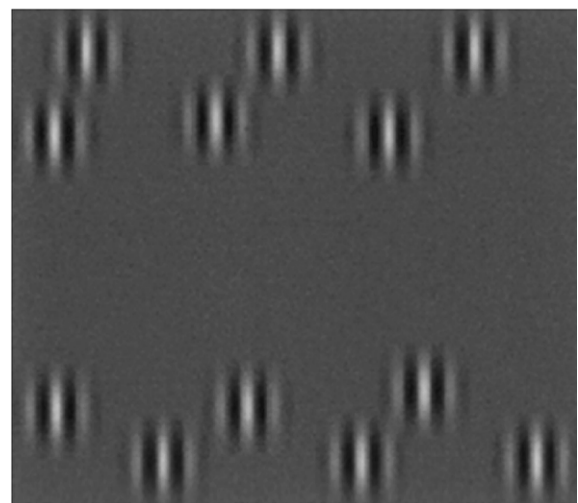

Fig. 1. The stimuli used for the two-exposure apparent motion Gabor micropattern kinematograms. Stimuli are represented in (a) for the linear motion condition and in (b) for the non-linear motion condition. Only the achromatic stimuli are shown.
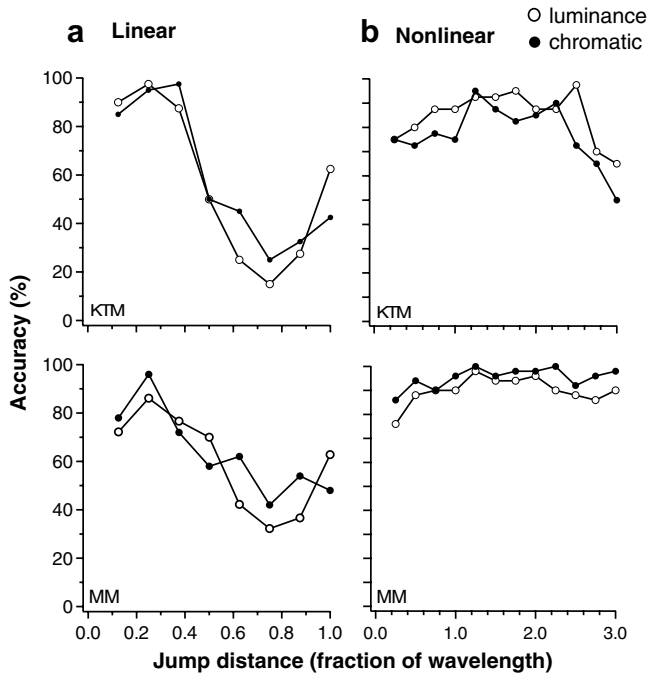
Fig. 2. Results illustrating the percentage of correct judgements of direction of motion with stimuli isolating (a) linear motion (seven Gabor micropatterns per row and SOA of 100 ms) and (b) non-linear motion mechanisms (three Gabor micropatterns per row and SOA of 150 ms) as a function of the jump distance for S-cone isolating (filled circles) and achromatic (open circles) Gabor micropatterns. The contrast of the stimulus was set to five times the detection threshold, which was determined using a 2AFC staircase method (for LA: 0.098, for MM: 0.096, for KTM: 0.11).

BARCO CCID RGB monitor was used, with a spatial resolution of 496×428 pixels, a frame rate of 150 Hz non-interlaced, and a mean luminance of 30 cd/m^2. The luminance output of the CRT guns is non-linear and was corrected with look-up tables using the VSG calibration system (OptiCAL, Cambridge Research Systems). The chromaticities of the red, green, and blue phosphors were measured using a Photo Research PR-700 PC Spectrascan.

2.2. Color space and S-cone isolation

Our chromatic stimuli were modulated along the S-cone axis of a three-dimensional cone contrast space (Noorlander & Koenderink, 1983; Stromeyer, Cole, & Kronauer, 1985; Cole, Hine, & McIlhagga, 1993; Sankeralli & Mullen, 1997), whose L-, M-, and S-cone axes are scaled in contrast units and so are independent of the mean luminance and chromaticity of the background. The S-cone axis is a cardinal direction under the definition by Cole et al. (1993), since it represents the stimulus direction that isolates the S-cone opponent (blue–yellow) postreceptoral detection mechanism from the other two (L/M-cone opponent and luminance mechanisms, respectively). The achromatic stimulus lies in the 1L+1M+1S direction (isochromatic) in (L, M, S) cone contrast space and represents the luminance cardinal direction.

We verified that our stimuli were effectively isolating the S-cone axis for each subject by using a perceptual task. A Gabor stimulus (with spatial frequency of 0.5 cpd) of fixed cone contrast was used and its direction in cone contrast space within the isoluminant plane was varied by the subject using a method of adjustment to find a minimum in perceived visibility. Thus maximum visibility occurs for the stimulus direction that lies closest to the direction of the L/M isoluminant cone opponent axis, and minimum visibility occurs when only the S-cone mechanism is activated and the L/M-cone opponent mechanism is silenced. For all our subjects the point of minimum visibility corresponded to the vector direction of the S-cone axis.
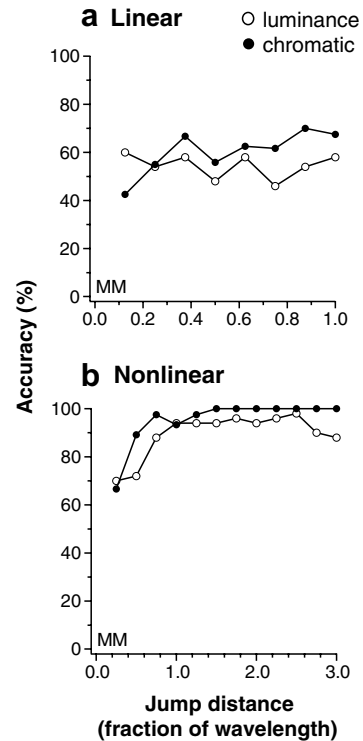

Fig. 3. Percent accuracy as a function of jump distance when Gabors are rotated by 90° between stimulus presentations, for stimulus conditions shown in Fig. 2, selected to isolate (a) linear, and (b) non-linear motion mechanisms. Results are presented for chromatic (filled circles) and achromatic (open circles) Gabor micropatterns.

2.3. Observers

Five observers participated in these trials, three experienced psychophysical observers (K.T.M., M.M., and T.Y.) and two observers naive to the purposes of the experiment (L.A. and W.M.). All had normal to corrected-to-normal visual acuity and normal color vision as assessed using the Farnsworth-Munsell 100-Hue test.

2.4. Stimuli

2.4.1. Gabor micropatterns in two-flash apparent motion

Linear and non-linear contributions to motion detection were separated by using different stimulus parameters in a two-flash apparent motion paradigm, as outlined in Baker et al. (1998), Boulton and Baker (1993a, 1993b), Clifford et al. (1998), and Yoshizawa et al. (2000). These stimuli were composed of rows of Gabor micropatterns (Fig. 1), which were presented in two bands for perifoveal viewing (either four or six degrees above and below the central foveal position) in order to avoid tracking of the motion of individual stimulus elements (Baker et al., 1998). Each stimulus was displayed for a short duration (100 ms), after which it was displaced to the left or right, with the same exposure duration as the first presentation. The presentations of the two stimuli were separated by a variable temporal delay termed the stimulus onset asynchrony (SOA). Stimuli were either S-cone isolating or achromatic.

The individual micropatterns were vertical Gabor patches, which consisted of a one-dimensional sine wave grating (carrier), enclosed in a smooth two-dimensional Gaussian contrast envelope:

$$G(x,y) = C\exp\left(-\left(x^2/2\delta_x^2 + y^2/2\delta_y^2\right)\right) \times \cos\left(2\pi(x\sin\theta + y\cos\theta)/\lambda\right),$$
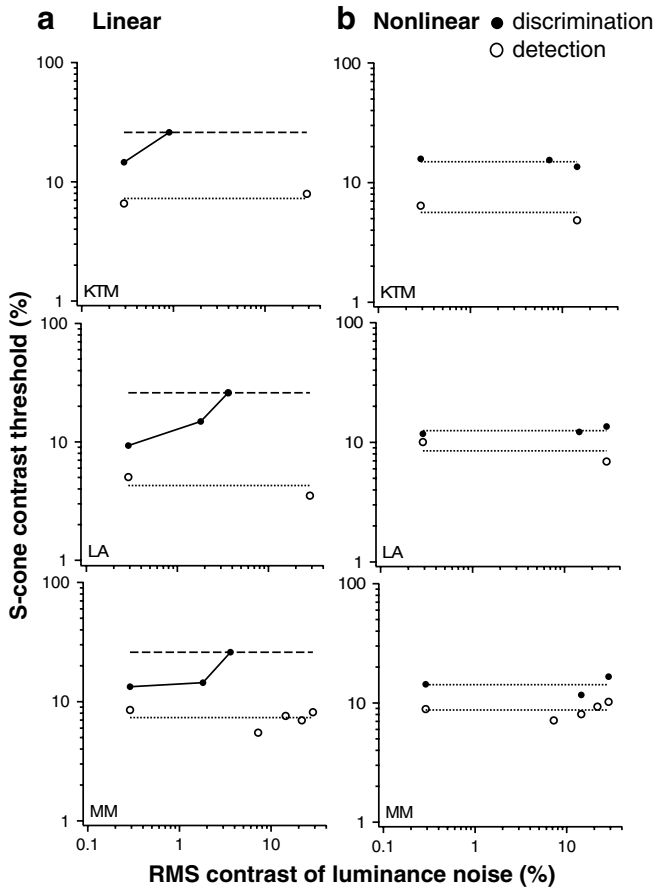
Fig. 4. Contrast thresholds for detection and discrimination of motion for S-cone isolating stimuli that stimulate (a) linear and (b) non-linear motion mechanisms, as a function of luminance noise contrast. Filled circles indicate direction discrimination thresholds and open circles detection thresholds. Fine dashed lines represent a linear fit to detection thresholds, and thick dashed lines indicate the highest monitor contrast available, beyond which no further thresholds could be measured.

where θ is the orientation of the carrier, C is the contrast, δ_x and δ_y are the parameters of the contrast envelope, and λ is the wavelength of the cosine wave. The values of δ_x and δ_y were fixed at $3/4\lambda$ and the spatial frequency at 1 cpd (cycles per degree).

In these experiments, we were not only interested in whether or not the motion discrimination and detection were performed using chromatic mechanisms, but also in understanding the nature of these mechanisms. We used stimulus parameters based on previous studies to isolate two separate motion mechanisms. The spatial and temporal properties of the stimuli were based on studies by Baker et al., 1998 and Yoshizawa et al., 2000. A high density of Gabor micropatterns (seven per row) and moving the pattern to the left or right by $1/4\lambda$ (0.25°) with a short stimulus onset asynchrony (SOA) of 100 ms, reveals the linear motion mechanism, whereas to isolate a non-linear motion mechanism we used a stimulus composed of a low density of Gabor micropatterns (three per row), displaced by $3/2\lambda$ (1.5°), with a long SOA (150 ms). These two-flash apparent motion stimuli were used in the first set of experiments (Figs. 2–8).

2.4.2. Drifting gratings

In the second set of experiments (Fig. 9), stimuli were horizontal isoluminant yellow–blue gratings with a spatial frequency of 0.75 or 1.5 cpd presented in a static Gaussian contrast envelope ($\sigma = 1.33°$). Stimulus contrast was ramped on and off in a raised cosine envelope with a total duration of 1 s. The temporal frequency of the drifting grating was varied between 0.75 and 6.0 Hz.
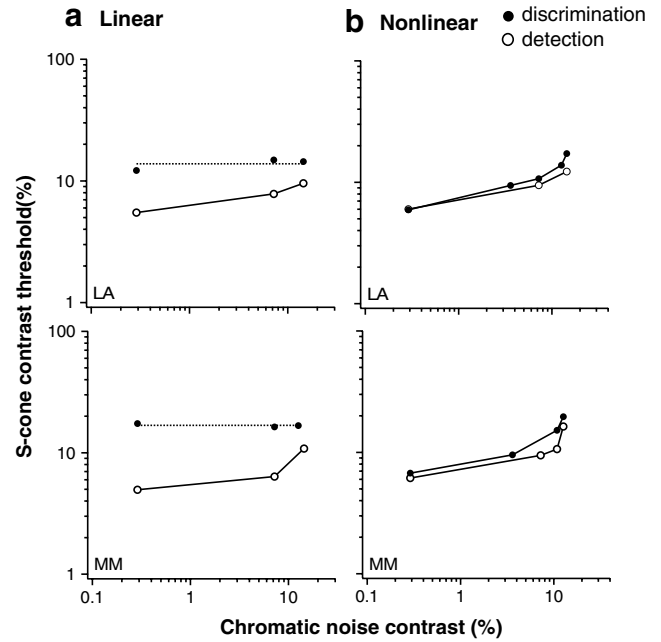

Fig. 5. Thresholds for detection and direction discrimination of drifting S-cone isolating Gabor micropatterns in the (a) linear and (b) non-linear motion condition, as a function of S-cone isolating, chromatic noise contrast. Filled circles indicate direction discrimination thresholds and open circles detection thresholds. Fine dashed lines represent a linear fit to detection thresholds.
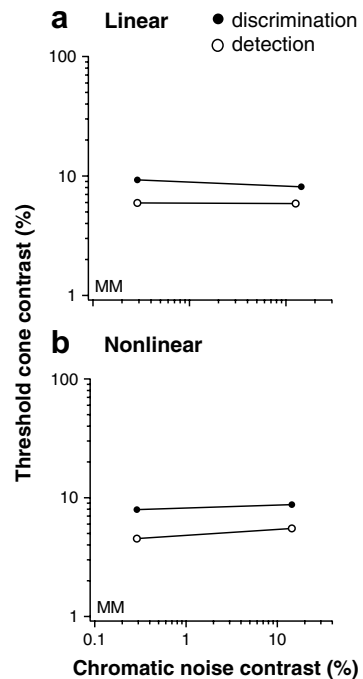

Fig. 6. Thresholds for detection and direction discrimination of achromatic Gabor micropatterns in the (a) linear and (b) non-linear motion conditions, as a function of S-cone isolating, chromatic noise contrast. Filled circles indicate direction discrimination thresholds and open circles detection thresholds.
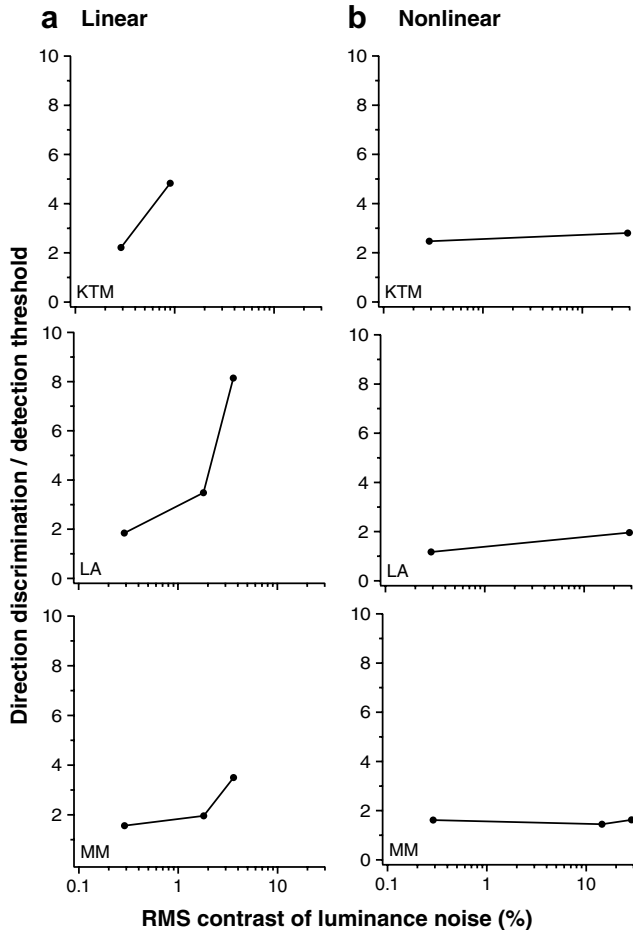
Fig. 7. Ratio of thresholds for direction discrimination to detection for Gabor micropatterns in the (a) linear and (b) non-linear motion conditions as a function of luminance noise contrast.
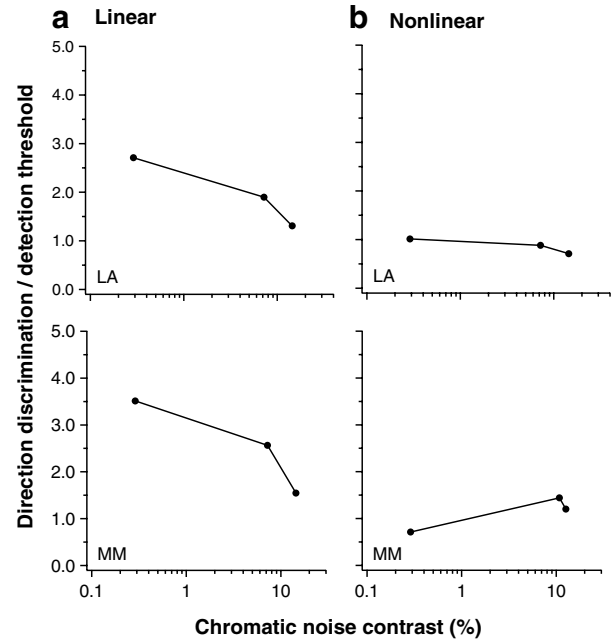

Fig. 8. Ratio of thresholds for direction discrimination to detection for Gabor in the (a) linear and (b) non-linear motion conditions, as a function of S-cone isolating, chromatic noise contrast.

2.5. Psychophysical procedure

For the two-flash Gabor micropattern stimuli, thresholds for both the detection of the stimulus and discrimination of its direction of motion were measured using the method of constant stimuli (MCS). In the detection task, we used the MCS with a two alternative forced choice (2AFC) task where the subject indicated using a button press which of the two intervals contained the stimulus (the other was a blank screen of mean luminance). In the direction discrimination task, a single interval was used and the subject indicated in which of two directions (left or right) the stimulus had moved in successive frames. A minimum of 50 trials were performed for each condition and psychometric functions were fitted to the data using a Weibull distribution function (Weibull, 1951), with threshold evaluated at the 81.6% accuracy level.

In the case of the single drifting Gabor, thresholds for detection of the stimulus and discrimination of its direction of motion were measured using a two alternative forced choice (2AFC) staircase procedure. Stimulus contrast was raised by 25% following an incorrect response, and lowered by 12.5% following two consecutive correct responses. A reversal was defined when the subject responded incorrectly after a minimum of two consecutive correct responses. Each staircase terminated after six reversals and the threshold value was calculated as the mean of the last 5 reversals of the staircase, corresponding to an 81.6% correct level. For each 2AFC staircase, the number of total trials fluctuated between 30–60 trials. This number guarantees reliable threshold

estimation based on the number of designated reversals (Rammsayer, 1992). Staircases were repeated 3–5 times. In the detection task subjects indicated which of two intervals contained the stimulus (the other was a blank screen of mean luminance) and audio feedback was used. In the direction discrimination task, a single presentation interval was used; the subjects indicated in which of two directions (left or right) the stimulus was drifting. A small fixation spot appeared before and after but not during stimulus presentation.

2.6. Luminance and chromatic noise masking

Previous studies have demonstrated the effective use of chromatic and luminance noise masking paradigms in determining whether chromatic or luminance mechanisms underlie thresholds (Gegenfurtner & Kipper, 1992; Losada & Mullen, 1994). It has been demonstrated that luminance noise is effective at masking luminance defined motion thresholds, and likewise chromatic noise is effective in masking chromatic motion thresholds (Yoshizawa et al., 2000). We superimposed luminance noise on our test stimuli (for both the two-flash apparent motion Gabor micropattern stimuli and drifting single Gabor stimuli) and measured thresholds for detection of the stimulus and discrimination of its motion. The luminance noise was spatially one-dimensional and temporally dynamic with a flat spatial and temporal Fourier amplitude spectrum. Chromatic noise was also superimposed on the Gabor micropattern (two-flash apparent motion) stimuli and thresholds for both detection and direction discrimination were measured using the method of constant stimuli. The chromatic noise was spatially one-dimensional, temporally dynamic, and was filtered with a spatially low-pass filter (Butterworth digital filter, as detailed in Yoshizawa et al., 2000) to reduce possible luminance artefacts from chromatic aberrations. This filter had a cut off frequency of 3 cpd, and reduced amplitude by 40 dB at 4 cpd. The noise contrast was defined by RMS contrast $C_{rms} = C/\sqrt{3}$ in screen contrast units and the maximum stimulus contrast available was 28.9%. The stimuli and luminance or chromatic noise were frame interlaced on a frame by frame basis and the noise was presented for 50ms before and after each stimulus presentation.

3. Results

3.1. Isolating linear and non-linear motion mechanisms

The first experiment was designed to investigate whether the stimuli could effectively isolate linear and non-linear motion mechanisms. The stimuli were presented in two-flash apparent motion and a paradigm developed initially for achromatic stimuli was used to determine whether first-order or higher-order motion mechanisms determine direction discrimination in which the direction discrimination is measured as a function of the magnitude of the displacement of the stimuli (Boulton & Baker, 1993a, 1993b; Boulton & Baker, 1991; Clifford et al., 1998). A series of interleaved trials were presented with the displacement

values varying for each presentation (between 0.125–1.0 λ for linear motion, and 0.25–3.0 λ for non-linear motion), and performance was measured as percent correct. The results are presented in Fig. 2, in which the percentage of correct responses in determining the direction of motion (using both linear and non-linear motion) is plotted as a function of the displacement, with filled circles representing results for chromatic (S-cone isolating) stimuli, and open circles those for luminance stimuli.

In Fig. 2a, stimulus conditions of a high micro pattern density (seven Gabors per row) and short SOA (100 ms) were used, which have previously been shown to be effective at isolating a linear motion mechanisms (Baker et al., 1998; Baker & Hess, 1998; Boulton & Baker, 1993a, 1993b; Boulton & Baker, 1991). Previously published
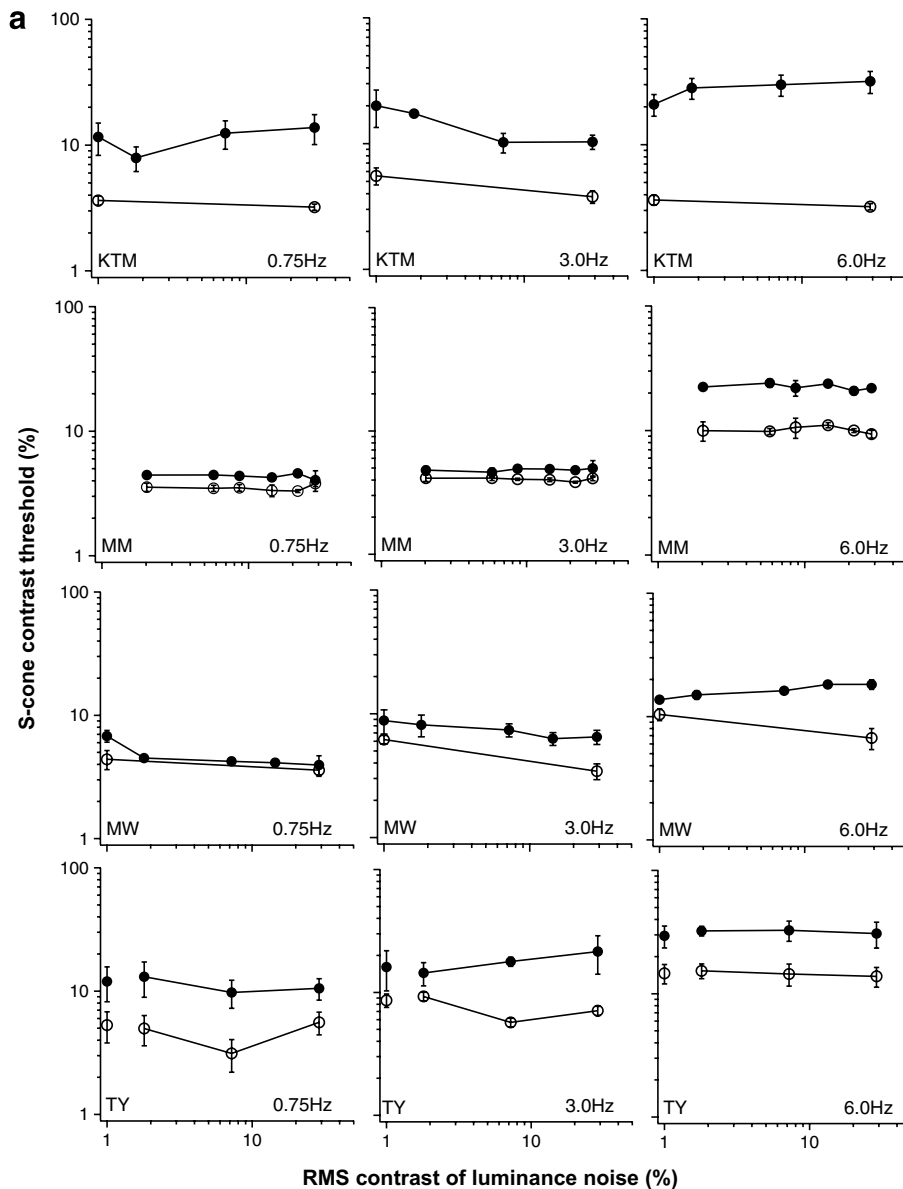

Fig. 9. Thresholds for detection and direction discrimination of a single, drifting S-cone isolating Gabor, as a function of luminance noise contrast, for spatial frequencies of (a) 0.75 cpd and (b) 1.5 cpd ($\sigma = 1.33°$), over a range of temporal frequencies from 0.75–6.0 Hz. Filled circles indicate direction discrimination thresholds and open circles detection thresholds.
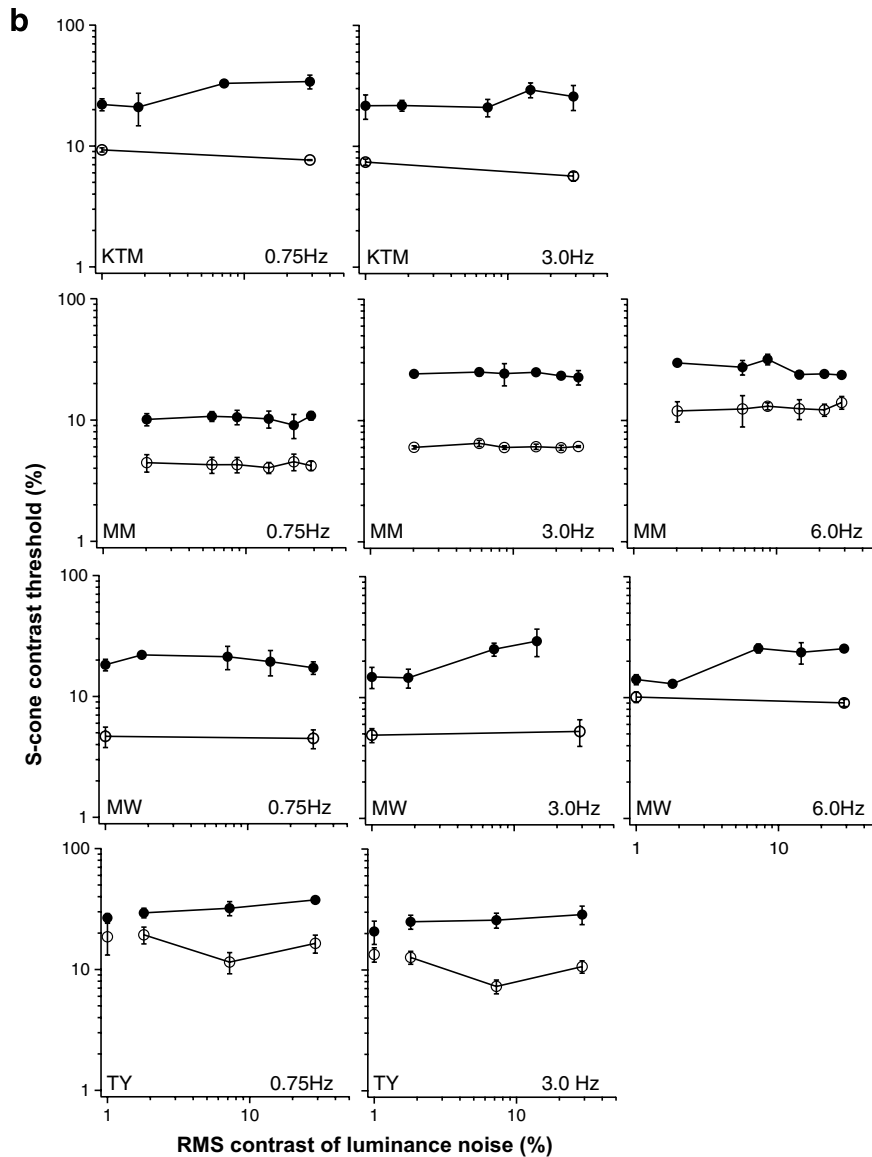
Fig 9. (*continued*)

results (Adelson & Bergen, 1985; Yoshizawa et al., 2000) with linear models predict that performance is cyclic with optimal performance at small displacements (near $1/4\lambda$) relative to the carrier wavelength. It is evident in the results in Fig. 2a, for both the S-cone isolating and the achromatic stimuli, that motion detection is optimal with a high density of Gabor micropatterns and a short SOA close to $1/4\lambda$, with chance performance at around $1/2\lambda$, and some motion reversal occurring between $1/2\lambda$ and 1λ. These performance profiles are as predicted from a linear motion detector (Baker et al., 1998).

In Fig. 2b, stimulus conditions were used with a lower micro pattern density (three Gabors per row) and longer SOA (150 ms) that are effective at revealing non-linear motion mechanisms (Baker et al., 1998; Baker & Hess, 1998; Boulton & Baker, 1993a, 1993b; Boulton & Baker, 1991). In the results of Fig. 2b we observe high accuracy of performance over a broad range of displacements

(above 1λ) for both the S-cone isolating and achromatic stimuli. This indicates that performance for a low density of Gabor micropatterns and a long SOA is mediated via non-linear motion mechanisms.

In order to ensure that we had effectively isolated both linear and non-linear motion mechanisms, we repeated the measurements for direction discrimination with the Gabor micropatterns rotated by 90° between successive stimulus presentations. Rotating the Gabors in this manner eliminates the contribution of a carrier-dependent linear motion mechanism, but has no effect on non-linear motion mechanisms such as those based on the contrast envelope of the Gabor stimuli. It is evident in Fig. 3a that for the linear motion stimulus, when the micropatterns are rotated by 90° between successive stimulus presentations, performance is around the chance level over a wide range of jump distances. This is evidence that our stimulus in Fig. 2a is dependent on the carrier and isolates a linear motion

mechanism. In contrast, for the case of the non-linear motion stimulus (Fig. 3b), performance is unaffected by the carrier rotation, supporting the conclusion that motion in Fig. 2b is mediated via non-linear mechanisms.

3.2. Luminance noise masking

We measured thresholds for the detection and direction discrimination of the S-cone isolating stimulus as a function of increasing luminance noise contrast for both linear (Fig. 4a) and non-linear (Fig. 4b) motion conditions, where open circles illustrate the detection thresholds and filled circles illustrate thresholds for direction discrimination. The results in Fig. 4a demonstrate that thresholds for detection of the stimuli are unaffected, but those for direction discrimination increase with increasing luminance noise contrast, until direction discrimination is impossible even at the highest monitor contrast available (represented by a dashed line). The elevation in these thresholds indicates a luminance contribution to motion thresholds for S-cone isolating stimuli under linear motion conditions, suggesting that they may be mediated by a luminance-based motion mechanism. In the case of non-linear motion (Fig. 4b), it is evident that luminance noise has no effect on detection or direction discrimination thresholds for S-cone isolating stimuli, indicating no luminance contribution to motion discrimination and that non-linear motion is therefore presumably mediated by chromatic mechanisms.

3.3. Chromatic noise masking

In order to test for a chromatic contribution to motion discrimination of the S-cone isolating stimuli, we repeated our previous measurements using S-cone isolating, chromatic noise. A threshold robust to chromatic noise but masked by luminance noise would indicate that a purely luminance based mechanism mediates the response, but one robust to luminance noise but sensitive to chromatic noise would indicate a purely chromatic motion mechanisms is mediating the response. It is also possible that a stimulus is masked by both chromatic and luminance noise, indicating a non-specific chromatic-luminance mechanism determines threshold. Possible hybrid color-luminance mechanisms have been suggested in different contexts (Baraas, 2005; Cavanagh & Anstis, 1991; Hawken et al., 1994). For example, Cavanagh et al. (1984) showed that adding chromatic contrast to a luminance grating decreases its perceived speed, suggesting that motion perception is a combination of processing from separate luminance and color motion systems. Hence, masking by chromatic noise will determine whether detection thresholds for linear and non-linear motion, and direction discrimination thresholds in the case of non-linear motion, are mediated by purely chromatic mechanisms or by hybrid color-luminance ones.

Fig. 5a shows that for the case of linear motion, detection thresholds for S-cone isolating stimuli increase with increasing chromatic noise contrast, but those for motion discrimination are unaffected, indicating that chromatic mechanisms mediate the detection of these stimuli but their motion discrimination is performed via luminance mechanisms. In the case of non-linear motion (Fig. 5b), thresholds for both detection and direction discrimination are elevated with increasing chromatic noise contrast, confirming that the detection of the stimulus and its motion discrimination are mediated by chromatic mechanisms.

As a control experiment to ensure that the S-cone isolating noise was purely chromatic in its effect, we measured thresholds for detection and direction discrimination of motion for achromatic stimuli in the presence of this chromatic noise for one subject (MM), since thresholds for detection and direction discrimination of achromatic stimuli should be unaffected by purely chromatic noise. The results in Fig. 6a illustrate that for linear motion, detection and direction discrimination thresholds are unaffected by the addition of increasing contrast S-cone isolating chromatic noise over the full contrast range. Likewise for the case of non-linear motion (Fig. 6b), both detection and direction discrimination thresholds are stable for a wide range of chromatic noise contrasts, confirming that the noise is purely chromatic and produces no luminance signals.

Furthermore, we note that the absence of a masking effect of the luminance noise on the chromatic stimuli under the non-linear motion conditions cannot be due to the spatial scale of the noise since chromatic noise with identical spatio-temporal properties to the luminance noise effectively masks non-linear motion.

3.4. Ratios

In order to summarise our data we plot the ratios of direction discrimination to detection thresholds for the S-cone isolating stimuli as a function of luminance masking noise (Fig. 7) and chromatic masking noise (Fig. 8) for both linear and non-linear motion results in the perifoveal position. For masking stimuli using luminance noise, it is evident that in the case of linear motion (Fig. 7a), the ratios between direction discrimination and detection thresholds increase with increasing luminance noise contrast, ranging from 1.6 at very low noise contrast to 8.2 at high noise contrast, reflecting the fact that there is a strong masking effect of luminance noise on direction discrimination thresholds, but none on detection thresholds. Therefore, luminance mechanisms mediate the discrimination of linear motion for S-cone modulated stimuli. For the case of non-linear motion (Fig. 7b), the ratios of direction discrimination to detection thresholds are stable (averaging 1.9 ± 0.3) over a large range of luminance noise contrasts, reflecting the fact that non-linear chromatic motion for S-cone isolating stimuli is robust to luminance noise for both detection and direction discrimination. We conclude that luminance mechanisms are not involved in the detection or the discrimination of the motion of these non-linear stimuli, these tasks being performed by chromatic mechanisms.

It can be seen in Fig. 8a that when linear motion is masked by chromatic (S-cone modulated) noise, the ratio of direction discrimination to detection thresholds decreases as the contrast of the chromatic noise increases. This reflects our finding (Fig. 5) that chromatic noise has a masking effect on detection thresholds of S-cone isolating stimuli but has no effect on direction discrimination for linear motion, consistent with chromatic mechanisms supporting detection but luminance mechanisms supporting linear motion thresholds. In contrast, for non-linear chromatic motion (Fig. 8b), the ratio of direction discrimination to detection thresholds remains relatively stable over a large range of noise contrasts (with an average value of 1 ± 0.2), indicating the effects of chromatic noise are equivalent for both detection and direction discrimination of non-linear motion of S-cone isolating stimuli, with small deviations from unity. We can therefore conclude that non-linear motion discrimination of S-cone modulated chromatic stimuli is mediated via chromatic mechanisms.

We conclude that for stimuli defined solely by isoluminant S-cone modulations, a chromatic system supports the discrimination of the motion of under non-linear conditions, however, luminance based mechanisms mediate motion discrimination for S-cone stimuli under linear motion conditions. The detection of S-cone isolating stimuli is performed via chromatic mechanisms.

One parameter that might affect the contribution of luminance signals to chromatic motion is that of stimulus speed. The work of Hawken et al. (1994) suggests that there are two motion mechanisms for chromatic motion discrimination, a chromatic based mechanisms for slow speeds and one for fast speeds which appears to have a luminance contribution. In our stimulus, for linear motion the speed of the stimulus is 2.5 deg/s, and that for non-linear motion is 10 deg/s. Therefore, their study would predict that we should find a luminance contribution to the direction discrimination of our non-linear stimulus, however we find to the contrary. In addition, Yoshizawa et al. (2000) demonstrated in a control experiment using the same stimuli as we use that stimulus speed did not affect the isolation of a luminance based linear and color based non-linear motion response for red–green (L/M-cone opponent) chromatic stimuli. We are therefore reasonably confident that our results may be generalized to other stimulus speeds.

3.5. S-cones mediate motion processing of drifting Gabors

Previous studies have illustrated that the motion of drifting isoluminant red–green gratings appears slower than their luminance counterparts (Cavanagh et al., 1984; Livingstone & Hubel, 1987; Mullen & Boulton, 1992a, 1992b; Troscianko & Fahle, 1988). This slowing has also been observed for blue–yellow gratings (Cavanagh et al., 1984; Dougherty et al., 1999), however, the motion of drifting S-cone isolating gratings has received little if any other attention. Having established that the motion of red–green drifting gratings is discriminated via luminance mechanisms (Mullen et al., 2003), the issue of whether chromatic or luminance based mechanisms mediate the motion of smoothly drifting blue–yellow gratings is still unresolved. Although, the motion of a single drifting grating (Gabor) is mediated by the carrier sinewave, it is still possible that non-linear motion mechanisms can contribute to direction thresholds, for example through tracking or attention mechanisms (Lu & Sperling, 1996; Lu & Sperling, 2001; Sperling & Lu, 1998). In order to elucidate whether chromatic or luminance motion mechanisms contribute to direction discrimination thresholds of an S-cone isolating grating, we measured detection and motion discrimination thresholds for a single S-cone isolating, smoothly drifting Gabor ($\sigma = 1.33°$) in the presence of increasing luminance noise contrast for relatively low spatial frequencies of 0.75 cpd (Fig. 9a) and 1.5 cpd (Fig. 9b), which should be free from chromatic aberration (Bradley, Zhang, & Thibos, 1992), and a range of temporal frequencies (0.75–6.0 Hz). We observed that thresholds for both detection (open circles) and motion discrimination (filled circles) are relatively unaffected by increasing luminance noise contrast (we observe only a slight increase for MW at 3.0 and 6.0 Hz). Therefore, we can assume that for drifting Gabor stimuli, both detection and motion discrimination are mediated via chromatic mechanisms. However, motion cannot be discriminated until we have reached high S-cone contrasts ($15.37 \pm 6.76\%$ for 0.75 cpd and $22.5 \pm 5.48\%$ for 1.5 cpd, averaged across all subjects and conditions), whereas, gratings can be detected at much lower thresholds ($8.02 \pm 3.10\%$ for 0.75 cpd and $5.9 \pm 3.59\%$ for 1.5 cpd).

4. Discussion

4.1. Chromatic non-linear motion for S-cones

We have demonstrated that we are able to stimulate both linear and non-linear motion mechanisms using S-cone isolating Gabor micropatterns presented in a two-flash apparent motion paradigm. We have found that the response of the visual system to the discrimination of motion of purely chromatic S-cone isolating stimuli depends on whether stimuli isolate a linear or non-linear motion mechanism. For stimuli that isolate linear motion, thresholds for motion discrimination are masked by luminance noise but are unaffected by chromatic nose, indicating that a luminance based system mediates linear motion discrimination. Conversely, for stimuli that isolate non-linear motion, direction discrimination appears to be purely chromatic since luminance noise has no effect on thresholds for motion discrimination, whereas chromatic noise elevates thresholds.

All detection thresholds are masked by chromatic noise but not by luminance noise indicating that a purely chromatic system is responsible for stimulus detection. This confirms that there are no detectable chromatic aberrations in the stimulus, since these would be expected to produce luminance artefacts that would be revealed by a masking effect of luminance noise on detection thresholds.

Moreover, even in the absence of noise masking, there is still a gap between detection and motion discrimination thresholds (a mean ratio of 2.37 +/− 0.97 in Figs. 7 and 8), which is similar to that reported previously for S-cone isolating stimuli (Cavanagh & Anstis, 1991; Lee & Stromeyer, 1989), and demonstrates that these stimuli are detected by non-directional, chromatic mechanisms.

The double dissociation described above that we find for motion thresholds between the effects of luminance noise (masking linear motion but not non-linear motion) and chromatic noise (masking non-linear motion but not linear motion) confirms that non-linear motion of S-cone isolating stimuli is performed via chromatic based mechanisms, whereas linear motion is performed via luminance based mechanisms. This is in agreement with previous studies that have found an absence of a chromatic linear motion mechanism for red–green isoluminant stimuli (Yoshizawa et al., 2000; Yoshizawa, Mullen, & Baker, 2003), and suggested linear motion for chromatic isoluminant red–green stimuli are susceptible to luminance noise masking and hence may not be truly chromatic (Cropper & Derrington, 1994; Dobkins & Albright, 1993). Therefore, the proposal that linear motion is absent in color vision can now be generalised for both L/M- and S-cone chromatic systems.

With good reason it has been previously been assumed that the only role of S-cones is to contribute to the chromatic blue–yellow or "primordial" color subsystem through cone opponent interactions with L- and M-cones (Mollon, 1989). Much of the previous literature, which is largely based on the measurement of detection thresholds, has supported the idea that the S-cones only contribute to the "blue–yellow" cone opponent process, making very little or no contribution to either the L/M (red–green) cone opponent system (Cole et al., 1993; Sakurai & Mullen, 2006; Sankeralli & Mullen, 1996; Stromeyer et al., 1998; Tansley & Boynton, 1976) or the luminance system (Eisner and MacLeod, 1980; Cavanagh & Anstis, 1991; Cavanagh, MacLeod, & Anstis, 1987; Lee & Stromeyer, 1989; Sankeralli & Mullen, 1996, 1997). This is why the S-cone axis has been considered a cardinal axis under the definition by Cole et al. (1993), and has used in the "cardinal color space" of Krauskopf, Williams, and Heeley (1982), under the assumption that S-cones activate only one of these three post receptoral mechanisms. While this framework remains consistent with our results for detection thresholds, which are purely chromatic for S-cone isolating stimuli, it is inconsistent with our results for motion thresholds. We find that S-cones contribute to motion via two different pathways: a non-linear motion mechanism via a chromatic pathway and a linear motion mechanism via a luminance pathway.

A chromatic contribution to higher-order motion has been well established for red–green stimuli (Cavanagh & Anstis, 1991; Cavanagh et al., 1984; Derrington & Henning, 1993; Livingstone & Hubel, 1987; Lu et al., 1999; Metha & Mullen, 1998; Metha et al., 1994; Mullen & Boulton, 1992a; Yoshizawa et al., 2000), and here we demonstrate that S-cones also contribute to higher-order motion

via a chromatic mechanism. Whether our S-cone chromatic motion thresholds are based on second-order motion processes that extract the contrast envelope, or higher-order processes that track motion (Cavanagh et al., 1984; Lu & Sperling, 1996, 2001) has not been addressed by these experiments, although we used perifoveal stimuli to mitigate against the tracking of individual Gabors in the kinematograms.

We find that S-cones also contribute to the detection of linear motion but via a luminance pathway. Lee and Stromeyer (1989), using grating stimuli, have also reported the contribution of S-cones to a luminance based directionally selective mechanisms. They argued, however, that the luminance based S-cone signal first passes through a spectrally antagonistic site, presumably using the early specialized S-cone opponent neurons of the retina, and subsequently combines with L- and M-cones in a motion based mechanism. The failure of the chromatic S-cone noise to mask the S-cone directional response in our data suggests that the motion thresholds are mediated by a separate pathway with no cone opponent stage to the psychophysical response. At the physiological level, we suggest that the luminance thresholds supported by the S-cone stimuli in our motion task could be based on the responses of the M cells since these have strong achromatic responses but low chromatic sensitivity (Hubel & Livingstone, 1990; Lee, Pokorny, Smith, Martin, & Valberg, 1990; Merigan, Katz, & Maunsell, 1991), and are thought to make a significant contribution to the cortical motion area MT (Merigan & Maunsell, 1993), which also has low chromatic sensitivity in primates (Saito, Tanaka, Isono, Yasuda, & Mikami, 1989; Zeki, 1974). Moreover, primate M cells receive some inputs from S-cones (Chatterjee & Callaway, 2002; Derrington, Krauskopf, & Lennie, 1984). Chatterjee and Callaway (2002) report that S-cones make a contribution of up to 10% of the equivalent achromatic input to primate M cells, and find no evidence that S-cones pass through a cone opponent stage prior to the M cell response. Recent evidence has also revealed an S-cone input to primate MT (Barberini, Cohen, Wandell, & Newsome, 2005; Seidemann, Poirson, Wandell, & Newsome, 1999). In addition, fMRI has shown a very weak responses of human MT+ to moving S-cone isolating stimuli compared to its achromatic or red–green responses (Mullen, Dumoulin, McMahon, Zubicaray, & Hess (2007); Liu & Wandell, 2005), which may reflect an MT response via a psychophysically achromatic pathway.

4.2. Motion discrimination for drifting S-cone isolating gratings

Many previous studies have investigated chromatic motion of red–green L/M-cone stimuli in the context of continuously drifting Gabor stimuli (Cavanagh & Anstis, 1991; Cavanagh et al., 1984; Derrington & Henning, 1993; Livingstone & Hubel, 1987; Lu et al., 1999; Metha & Mullen, 1998; Metha et al., 1994; Mullen & Boulton,

1992a; Yoshizawa et al., 2000), and it has been demonstrated that motion discrimination for drifting red–green gratings is performed via luminance mechanisms (Mullen et al., 2003). In contrast, little attention has been paid to studies on motion discrimination focussed on smoothly drifting S-cone gratings (Cavanagh et al., 1984; Dougherty et al., 1999), and the role of S-cones in motion discrimination is still unclear, with conflicting reports that S-cones are not effective at motion discrimination (Cavanagh et al., 1984), but support global motion (Ruppertsberg et al., 2006). We have demonstrated that, in contrast to the results for red–green gratings, thresholds for detection and direction discrimination of smoothly drifting blue–yellow gratings are not masked by luminance noise, indicating that there is little if any luminance contribution to motion discrimination and that chromatic mechanisms mediate both motion discrimination and stimulus detection. Although, we cannot completely assume that there is no linear motion component mediating grating motion, our results imply that the contribution of the chromatic non-linear component of the stimuli is a likely mediator of motion discrimination and determines motion thresholds, since we have demonstrated that only discrimination of non-linear motion for S-cone isolating stimuli is robust to luminance noise. We propose that motion discrimination may be performed via non-linear mechanisms such as feature tracking or other higher-order processes (Seiffert & Cavanagh, 1999), as has been suggested also for isoluminant red–green gratings where subjects report that the motion appears jerky resembling that of apparent motion stimuli (Cropper, Mullen, & Badcock, 1996; Mullen & Boulton, 1992a). The differences between the results for red–green and blue–yellow drifting Gabors lead us to conclude that motion discrimination for L/M- and S-cone isolating gratings is performed via distinctly different processes. Isoluminant red–green patterns may also produce internal luminance intrusions owing to differential delays between red and green cone signals (Stromeyer et al., 1995), termed temporal chromatic aberration (Mullen et al., 2003), a delay that may be more pronounced than for the blue–yellow gratings, made up of a combination of S- and L/M-cone signals (Lee & Stromeyer, 1989). Furthermore, we note that the gap between detection thresholds, and motion discrimination thresholds is higher for smoothly drifting S-cone gratings compared with that for two-flash apparent motion (Lee & Stromeyer, 1989), which may be due to a weaker luminance component relative to the chromatic component in the drifting grating stimulus. Therefore, for gratings, direction discrimination may be processed by higher-order, chromatic motion mechanism, although the S-cone contrast thresholds for this motion are high.

5. Conclusions

We have used a protocol for isolating linear and non-linear motion in order to investigate the role of S-cones in motion processing. We have found that S-cones contribute to motion via two different pathways: a non-linear motion mechanism via a chromatic pathway and a linear motion mechanism via a luminance pathway. The luminance based residual linear motion may be mediated by an S-cone contribution to the M cell pathway (Chatterjee & Callaway, 2002). We have also demonstrated that for S-cone isolating drifting Gabors, there is no significant luminance contribution to motion discrimination, suggesting motion at threshold is mediated by non-linear higher-order mechanisms. This contrasts to drifting red–green isoluminant Gabors which reveal a significant luminance response (Mullen et al., 2003).

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